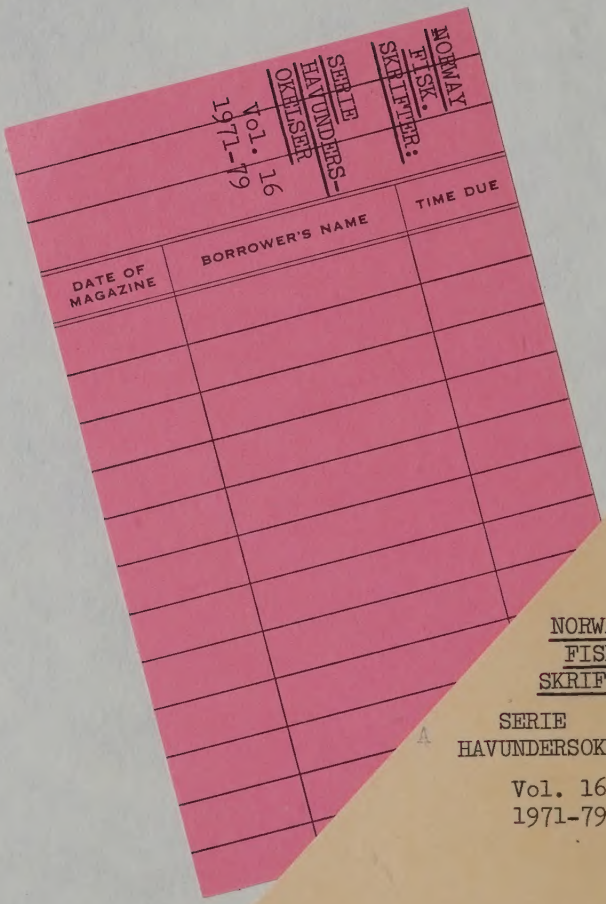

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SOVIET TAGGING OF HARP AND HOODED SEALS IN THE NORTH ATLANTIC

By

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ABSTRACT

Popov, L. A. 1970. Soviet tagging of harp and hooded seals in the North Atlantic. *FiskDir. Skr. Ser. HavUnders.*, *16*: 1—9.

In 1960—1968, 2 705 harp seal pups and 55 adult female harp seals were tagged in the White Sea. At Newfoundland 79 harp seal pups were tagged in 1963, and in the Jan Mayen area of the Greenland Sea 50 hooded seal pups were tagged in 1966. Monel metal clip tags were used in two seasons, but coloured plastic tail tags have been in use since 1965.

Early recaptures have shown that the northward drift of the pack ice brings the pups from the White Sea to the southern part of the Barents Sea. In some years, however, adverse conditions may change this drift pattern. Recaptures after one and two years indicate that immature harp seals spend the winter in coastal waters of the southern Barents Sea and the northern White Sea.

Two pups tagged off Newfoundland have been recaptured in West Greenland during their first summer.

INTRODUCTION

As part of an extensive Soviet research program, harp seals, *Pagophilus groenlandicus* (Erxleben, 1777) and hooded seals, *Cystophora cristata* (Erxleben 1777) have been tagged in the White Sea since 1960, in the Jan Mayen area of the Greenland Sea in 1964 and 1966 and off Newfoundland—Labrador in 1963. The taggings have been carried out by scientists from VNIRO Moscow, PINRO Murmansk and Sev-PINRO Arkhangelsk in accordance with programs approved by the Sealing Commission for the Northeast Atlantic.

The taggings by Soviet scientists supplement Canadian taggings at Newfoundland (Sergeant 1965) and Norwegian taggings at Newfoundland, in the Greenland Sea and in the Barents Sea (Rasmussen and Øritsland 1964). This paper summarizes data on Soviet taggings from 1960 to 1968 and reports the recoveries of tagged seals up to April 1969.

Table 1. Soviet seal pup taggings in 1960—1968 and recoveries up to April 1969.

Year of tagging	Series	Number tagged	Recoveries	
			Same Year	1—2 years later
Harp seals, White Sea.				
1960—1962	BM	45	0	0
1963	A	495	0	1
1964	A	105	0	0
1965	B	410	8	1
1966	B6	598	21	1
1967	B7	389	3	1
1968	B7	718*	14	0
Sum		2 760**	46	4
Harp seals, Newfoundland.				
1963	N	79	4	0
Hooded seals, Greenland Sea.				
1964	—	10	2	0
1966	G6	50	4	0
Sum		60	6	0
Total		2 899	56	4

* 168 pups tagged by «Chistopol» not included.
** 55 adult females included.

TAGGINGS AND TAGGING METHODS

The number of seals tagged in the different areas are listed by year in Table 1. The greatest number, 2 760 harp seals, has been tagged in the White Sea. In 1960—1964, 645 harp seal pups were tagged in areas where the sealers were operating, but in 1965—1968 when sealing from vessels was prohibited in the White Sea and only coastal dwellers were allowed to hunt, the taggings were made outside the hunting areas. In 1965, 410 pups were tagged from a research vessel. In 1966, 1967 and 1968, 1 650 pups and 55 adult females were tagged from the «Toros» stations on the drifting pack ice. The first two years thin 20 mm wide plastic tags (series BM) were attached to the tails with a wire. These tags were fragile and the attachment was not good enough so they were substituted by other types. Clip tags of monel metal (fur seal type, Fig. 1A) were used in 1963 and 1964. These tags were applied to the web of a hind flipper by special pliers. Because of their colour the metal

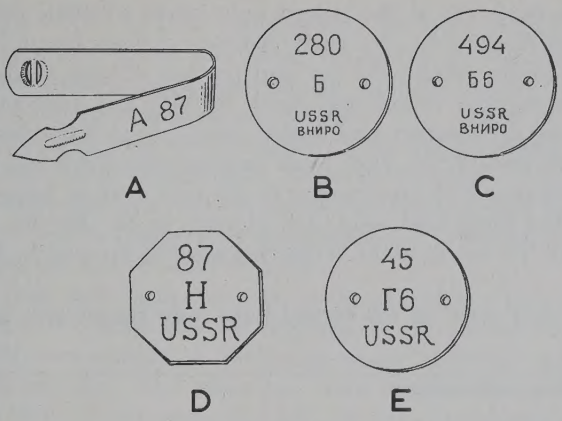

Fig. 1. Tag types used in Soviet taggings in: A, B and C) The White Sea, D) the Newfoundland area, E) the Jan Mayen area of the Greenland Sea.

tags are not easily discovered on harp seals, and may be overlooked by hunters. They also may cause inflammation with subsequent shedding of the tags. The use of the clip tags therefore was discontinued. In the following years (1965—1968) circular tags of red plastic, 2.5—3.0 mm thick and 32 mm wide, have been used (series B, B6 and B7 — USSR VNIRO, Fig. 1, B and C). These tags are attached to the tails of the seals with stainless wire, treated with a penicillin ointment, by piercing the tail with special needles.

In the Front area off Newfoundland—Labrador, 79 harp seal pups were tagged by an experimental Soviet sealing expedition in March 1963. Orange octahedral tail tags, 2.0 mm thick and 30 mm wide, were used (series N — USSR, Fig. 1D).

Except for a small number tagged with metal clips in 1964 (not included in Table 1), harp seals have not been tagged in the Greenland Sea. In 1966, however, scientists onboard the research vessel «Chistopol» succeeded in tagging 50 hooded seal pups in this area using tail tags of red plastic (series G6 — USSR, Fig. 1E).

RECOVERIES

All recovered tags are listed in the appended Table I, and the recaptures from the White Sea taggings are shown in Fig. 2. No early recoveries were reported from the taggings in 1960—1964. In 1965 Soviet vessels did not hunt in this area, and recoveries in that season were reported only by Norwegian vessels hunting in the Barents Sea.

The recaptures, 2.0%, of the tagged pups, were all made during the second half of April in the area north and west of Cape Kanin Nos.

In 1966 strong winds kept the pup patches drifting in the White Sea basin throughout March and April. In May and June pups were observed along the southern and western parts of the White Sea shores. All early recoveries, 3.5%, were made among pups which had perished from exhaustion or had been caught in fish nets in these areas in May and June. The northward migration of pups to the Barents Sea did not start until the mouth of the White Sea was free from ice in June and July.

In 1967 only three of 389 tagged pups were recaptured. Southerly

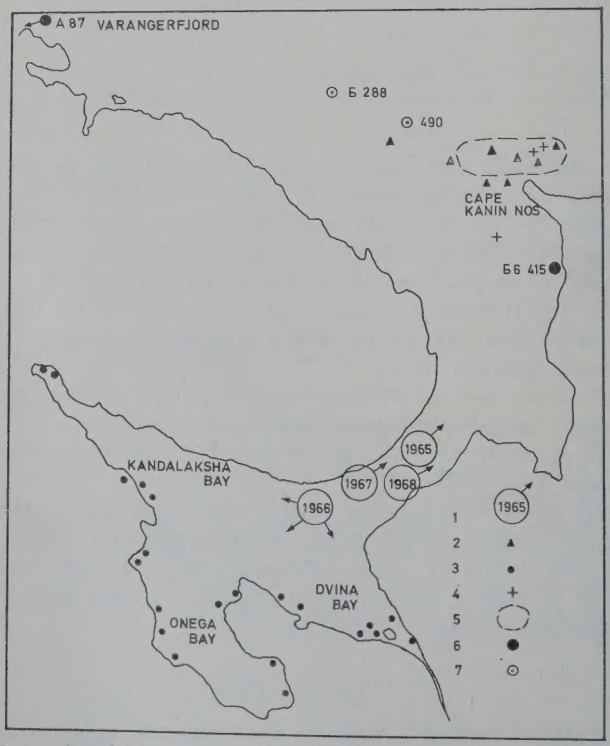

Fig. 2. Recoveries of harp seal tags from the White Sea. 1) Tagging locality and direction of passive migration, 2) recoveries in the tagging season 1965, 3) recoveries in the tagging season 1966, 4) recoveries in the tagging season 1967, 5) recoveries in the tagging season 1968, 6) recoveries in winter after 1—2 years, 7) recoveries in spring after 1—2 years.

winds kept the ice and the breeding lairs drifting northwards, and the tagged pups were found near Cape Kanin Nos by the research vessel «Chistopol» in early April, some 25 days after the tagging. No tags were returned from Norwegian sealers in 1967.

In 1968, 718 pups were tagged. Again the prevailing winds and currents sent the pups drifting to the north. After 30—35 days the pups were in international waters where the Norwegian vessels were hunting. Norwegian sealers reported 14 recaptures, 1.9%, outside Cape Kanin Nos during the first ten days of April.

Four harp seals tagged as pups in the White Sea, have been recaptured one or two years after the tagging (Fig. 2). Two of these (Nos. 490 and B288) were caught in the spring among moulting immature seals in the Barents Sea. The other two were caught in coastal waters in January 1968: a one-year-old (A67) in the Varangerfjord, Norway, and a two-year-old (B6 415) on the west coast of the Kanin Nos Peninsula.

Of the 79 harp seal pups tagged off Newfoundland in 1963, only

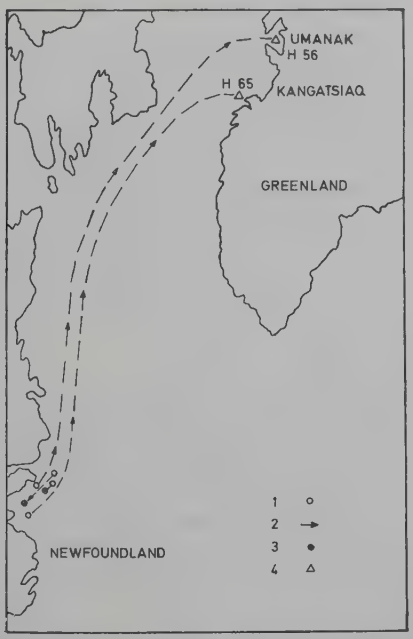

Fig. 3. Recoveries of harp seal tags from the Newfoundland area. 1) Tagging localities, April 1963, 2) assumed migrations, 3) early recoveries, 4) recoveries in July and August.

4 (5.1%) have been recaptured. Tagging localities and recoveries are shown in Fig. 3. Two tags were recovered by Canadian sealers in the same area 7 and 17 days after the tagging, and two were found on the West Greenland coast in July and August the same year.

In the Jan Mayen area of the Greenland Sea only four (8.0%) of a total of 50 hooded seal pups have been recaptured. They were all caught in the same area the same month.

DISCUSSION

The recoveries of harp seals tagged in the White Sea show that pups move passively with the drifting pack ice during the lactation period and for some time after weaning. This drift which is influenced by currents and winds in the area, usually has a northward direction and brings the pups out to the Barents Sea during April. In some years, however, constant and strong northerly winds in March and April may move the pack ice southwards, bringing the pups to the southern shores of the White Sea (e.g. 1966).

The duration of the passive northward migration of pups from the southern part of the White Sea estuary where they are born, to the Kanin Nos area depends upon the velocity of the ice drift in March. Constant and strong winds may move the pup concentrations past Cape Kanin Nos in 20—25 days, whereas the drift may take 40 50 days in years with variable winds. The passive migration to the Barents Sea brings the pups to areas with a rich food supply at the time when they are ready to start independent feeding. However, in years with a southward ice drift the pups are brought to areas of the White Sea which are poor in suitable food organisms. This will seriously impair the condition of the animals and may eventually lead to a heavy mortality among the pups as observed in 1966.

The recaptures of immature seals off the Kanin Nos Peninsula and in the Varangerfjord in January indicate that immature harp seals spend the winter i coastal waters of the Barents Sea and the northern White Sea. Independent observations show that they are feeding intensively on polar cod, *Boreogadus saida* (Lepechin, 1773), at this time of the year. Also adult seals are found feeding in coastal waters near Cape Kanin Nos during winter. In February the adult seals move towards the southern parts of the White Sea where they continue to feed until the breeding season.

The immature seals which were recaptured in the Barents Sea in April—May, were found in patches of moulting seals in the area where the White Sea harp seals usually stay during their moult.

The recaptures of harp seal pups in the Northwest Atlantic in 1963 support results of Canadian and Norwegian taggings off Newfoundland (Sergeant 1965, Rasmussen and Øritsland 1964). During lactation and for some time after weaning the pups move passively with the drift of the ice. Later they migrate northwards to their summer range in West Greenland (Sergeant 1965).

Recoveries of tags from hooded seal pups in the Greenland Sea in 1966 illustrate the early dispersal of pups in that area (Rasmussen and Øritsland 1964). The pups had moved in directions between north-north-west and southwest and were recaptured from 7 to 17 days after the tagging and from about 50 to about 110 nautical miles from the tagging localities.

ACKNOWLEDGEMENT

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Table I. Seal tags recovered up to April 1969 from Soviet taggings in the White Sea, off Newfoundland and in the Greenland Sea 1960—1968.

Tag No.	Tagging		Recovery	
	Date	Locality	Date	Locality
Harp seals, White Sea and Barents Sea.				
490.....	17 March 63	65°41'N 39°22'E	3May 65	68°55'N 41°00'E
BM 33.....	11 » 65	66°44'N 39°58'E	17 April 65	69°10'N 44°10'E
B 83.....	13 » 65	66°25'N 41°11'E	23 » 65	Kanin Nos area
B 158.....	»	»	26 April 65	69°00'N 42°38'E
B 183.....	»	»	22 April 65	68°51'N 41°48'E
B 193.....	»	»	April 65	Kanin Nos Area
B 211.....	»	»	» »	» » »
B 269.....	»	»	23 April 65	» » »
B 280.....	»	»	25 April 65	69°06'N 39°53'E
B 288.....	»	»	19 April 66	70°10'N 37°15'E
B6 494.....	3 March 66	65°40'N 38°00'E	15 May 66	66°34'E 34°00'E
B6 511.....	»	»	23 May 66	64°05'N 38°00'E
B6 313.....	»	»	5 June 66	Kandalaksha
B6 339.....	»	»	7 June 65	Dvina River delta
B6 380.....	»	»	June 66	Kandalaksha
B6 558.....	»	»	»	64°45'N 34°45'E
B6 4.....	13 March 66	65°20'N 38°05'E	27 June 66	64°56'N 36°20'E
B6 190.....	»	»	»	65°22'N 34°20'E
B6 387.....	»	»	June 66	65°00'N 36°40'E
B6 415.....	»	»	10 Jan. 68	67°42'N 44°00'E
B6 483.....	»	»	June 66	65°55'N 34°45'E
B6 595.....	»	»	4 June 66	64°15'N 34°30'E
B6 ?	?	?	June 66	64°40'N 35°00'E
B6 421.....	18 March 66	65°10'N 37°50'E	»	65°55'N 34°45'E
B6 168.....	»	»	15 June 66	?
B6 129.....	»	»	1 June 66	Dvina River delta
B6 179.....	24 March 66	65°10'N 37°50'E	June 66	65°22'N 34°30'E
B6 389.....	»	»	23 May 66	Dvina River delta
B6 547.....	»	»	6 June 66	» » »
B6 533.....	»	»	16 June 66	64°22'N 37°35'E
B6 ?	?	?	June 66	65°00'N 37°45'E
B6 ?	?	?	»	64°26'N 35°20'E
A67	March 67	White Sea	16 Jan. 68	Varangerfj., Norw.
B7 136.....	7 March 67	66°15'N 39°40'E	3 April 67	69°06'N 44°09'E
B7 145.....	»	»	»	69°06'N 44°10'E
?	?	?	»	68°17'N 43°02'E
B7 427.....	4 March 68	66°10'N 41°00'E	7 April 68	69°—69°15'N 42°—44°E
B7 465.....	»	»	11 April 68	»
B7 490.....	5 March 68	66°15'N 41°50'E	»	»
B7 500.....	4 March 68	66°10'N 41°00'E	»	»
B7 503.....	»	»	»	»

Table I (contd.) Seal tags recovered up to April 1969 from Soviet taggings in the White Sea, off Newfoundland and in the Greenland Sea 1960—1968.

Tag No.	Tagging		Recovery	
	Date	Locality	Date	Locality
B7 504.....	4 March 68	66°10′N 41°00′E	10 April 68	69°—69 15′N 42°—44°E
B7 513.....	»	»	7 April 78	»
B7 518.....	»	»	»	»
B7 547.....	»	»	»	»
B7 625.....	5 March 68	66°15′N 41°50′E	»	»
B7 699.....	»	»	?	»
B7 985.....	10 March 68	66°45′N 42°20′E	10 April 68	»
B7 1101.....	11 March 68	66°30′N 42°10′E	»	»
B7 ?	?	?	»	»
Harp seals, Northwest Atlantic.				
N 6.....	10 March 63	52°00′N 54°42′W	20 April 63	White Bay, Newfoundland
N 56.....	22 March 63	51°20′N 53°06′W	10 Aug. 63	70°50′N 52°00′W
N 60.....	»	51°23′N 53°06′W	March 63	Same area.
N 65.....	19 March 63	50°20′N 55°04′W	July 63	approx. 68°21′N 53°20′W
Hooded seals, Greenland Sea.				
G6 07.....	2 April 66	70°00′N 11°05′W	19 April 66	69°50′N 16°00′W
G6 13.....	»	»	9 April 66	70°45′N 14°20′W
G6 33.....	3 April 66	70°12′N 11°05′W	19 April 66	69° N 15° W
G6 45.....	»	»	»	70°54′N 12°10′W

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INVESTIGATIONS ON EUPHAUSIIDS IN SOME FJORDS ON THE WEST COAST OF NORWAY IN 1966 — 1969

By

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ABSTRACT

Wiborg, Kr. Fr. 1970. Investigations on euphausiids in some fjords on the west coast of Norway in 1966—1969. *FiskDir. Skr. Ser. HavUnders.*, *16*: 10—35.

In 1966—1969 euphausiids (krill) were sampled in some fjords in Western Norway. Drained volumes of krill constituted 13—82 ml, exceptionally 100—167 ml per 1 000 m³. *Meganyctiphanes norvegica, Thysanoessa inermis* and *T. raschii* dominated in the order mentioned. During the day, *Thysanoessa spp.* kept at higher levels than *M. norvegica;* during the night *T. raschii* and part of the stock of *M. norvegica* accumulated close to the surface. *M. norvegica* had densities of 0.1—1 specimens per m³, but higher concentrations were induced in spring with electric light. Vertical layering was observed with large specimens at deeper levels. *M. norvegica* spawned in March—June one year old. Part of the stock survived a second spawning, a few lived for nearly three years. One year olds measured 22—31 mm (average 27 mm), two year olds 32—41 mm (average 37 mm) and three year olds 43—47 mm.

In *T. inermis* a maximum of 1—4 specimens per m³ occurred in the upper 10—50 m during the night in January—February and October—November, at other times only 0.05—0.3 specimens per m³. *T. inermis* is annual in the area, spawning in March—June, with maximum in April. Length of one year olds was 17—20 mm, single second year survivors 26 mm. The two-spined form was observed in 1—3% of the stock.

T. raschii had maximum densities of 3.5 and 5.0 specimens per m³ in the upper 10 m in February and November respectively, at other times figures were very low. *T. raschii* is annual; spawning occurs in April—June, starting somewhat later than in *T. inermis*. Growth and length distributions are as a rule similar to those of *T. inermis*.

INTRODUCTION

During the later years attention has been focused on euphausiids or krill as a source of marine protein that may be exploited commercially. In Norway a small-scale fishery started in 1965, the krill mainly being used in fish farming. The biology of krill in fjords of Western Norway has been studied since 1965 (Wiborg 1966, 1968).

MATERIAL AND METHODS

In the period 21 November 1966—29 January 1969 samples of krill were collected from the R/V «Peder Rønnestad». A three-foot

Isaacs—Kidd midwater trawl (IKMT), mesh size three mm, was towed at four knots for 10—25 minutes at different levels between the surface and 260 m in some fjords on the west coast of Norway (Fig. 1). The Byfjord near Bergen was visited most regularly, with monthly samples in the period January—June. The depths fished were checked occasionally with a Benthos depth recorder. Most hauls were made during the night. Figures have been adjusted to 1 000 m^3 filtered. Additional hauls were made with Clarke-Bumpus plankton samplers (CB), mesh size 0.5 mm, speed 2—3 knots, in the upper 40 m, and some

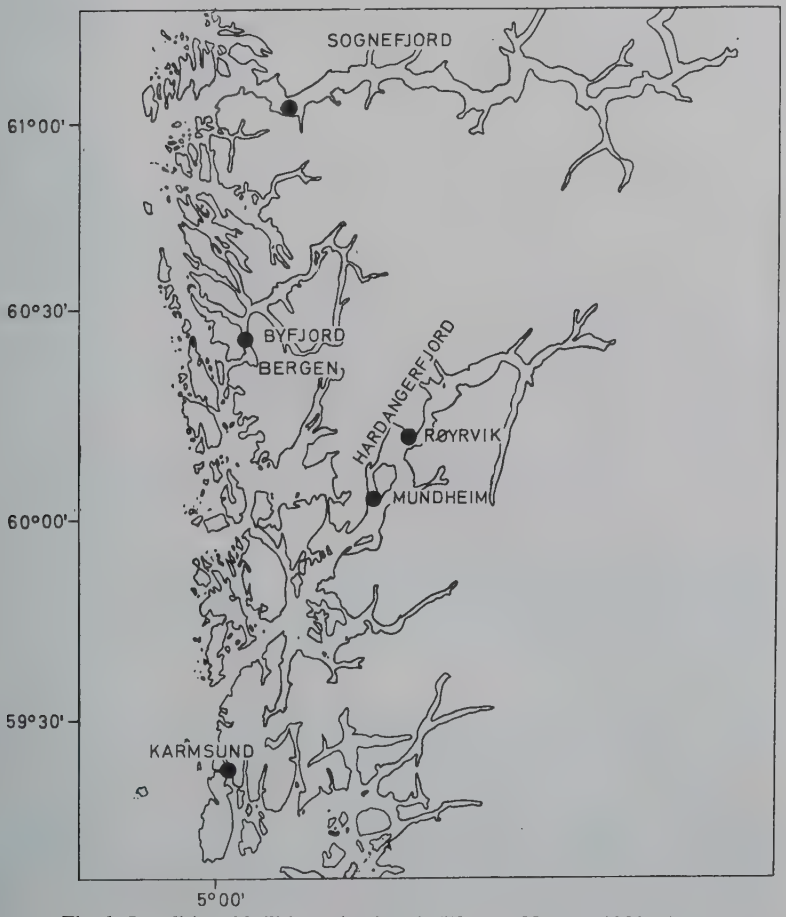


Fig. 1. Localities of krill investigations in Western Norway 1966—1969.

vertical hauls with a 40 cm Juday net, mesh size 0.2 mm, from bottom to surface. A few samples were also taken with light and ketcher in the Hardanger fjord. During the cruises bathythermograph casts were made to 260 m, and salinity and temperature were measured in the upper 60 m with a portable «salinity-temperature bridge».

In 1969 additional material was collected in the Byfjord during monthly cruises in day hauls with IKMT and a low-speed midwater trawl designed by Beyer (in preparation). The samples were preserved in 5—10 percent formalin and examined a few days after the catch. The krill and mysids were sorted out and their displacement volume measured together, then investigated under a stereoscopic microscope, and finally the total length was measured under a 2 X magnifying lens (Wiborg 1966). When the sex could be determined from external characters, males and females were measured separately.

TOPOGRAPHY AND HYDROGRAPHY OF THE BYFJORD AND THE HARDANGERFJORD

The Byfjord (Fig. 2) is part of a fjord system; in the southwestern part with a sill depth of 140 m towards the Hjeltefjord; in the north with connection to the Salhusfjord and Herdlefjord, the latter in the northwest ending in shallow sounds less than 10 m deep. The Byfjord has a central trough, 317—383 m deep. According to Linde (1970) the temperature below 100 m is usually 7.0—8.2 C, the salinity 33.34—34.90 $^0/_{00}$. Below 200 m the water is renewed each year, as a rule in November—February.

In 1966—1968 the temperature of the upper 10 m reached 15 C in June, the 10 C isotherm descending to 50 m in November 1966 and October 1967. At the surface the extreme temperatures were 3.6 C in January 1967 and 15.1 C in June 1967.

Below 10 m the salinity was usually 30 $^0/_{00}$ or more. At 5 m the lowest figure was about 22 $^0/_{00}$ in October 1967, otherwise close to 30 $^0/_{00}$. At the surface, there were records of about 10 $^0/_{00}$ and 18 $^0/_{00}$ respectively in June and October 1967.

The topography and hydrography of the Hardangerfjord (Fig. 1) has been described by Sælen (1962, 1967). There is a sill of 150 m in the outer part, and maximun depths of more than 900 m are found in the middle fjord. At the surface the water is sometimes very brackish, especially in the inner fjord during summer and autumn. Below 20 m the salinity is above 30 $^0/_{00}$ all the year, in the deeper layers 34.4—35.5 $^0/_{00}$. Temperature below 100 m is 6.5—8.0 C all the year, at the surface 2.5—15.7 C.

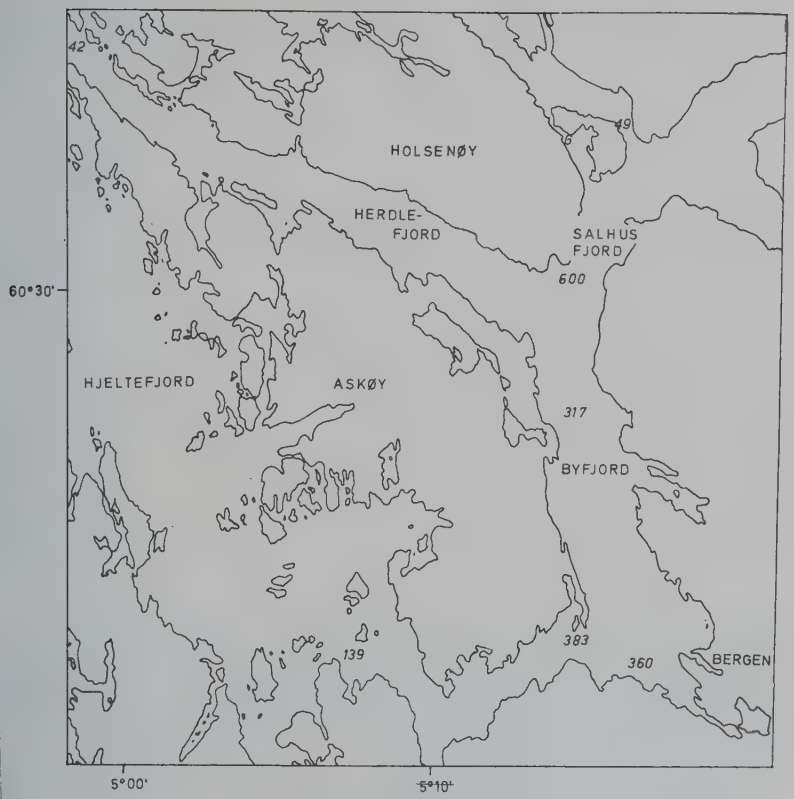


Fig. 2. The Byfjord and adjacent areas. Depths in m.

During the present investigation the extreme temperatures at the surface in the middle of the fjord were 4.9 and 16.6 C in March and June respectively, with the corresponding salinities of 30.4 ‰ and 12.2 ‰.

VARIATIONS IN THE VOLUMES OF KRILL AND MYSIDS IN 1967—1969

With a mesh size of three mm in the net of the IKMT some of the smaller krill will probably pass through the meshes. As the hauls were taken without any closing, the conclusions as to the vertical distribution must be taken with some precaution. However, the time of hauling in of the net was usually short as compared to the fishing time, and it

Table 1. Volumes of krill and mysids in ml per 1 000 m³ in the Byfjord near Bergen 1967—1969. 3' IKMT, mesh size 3 mm, trawling speed 4 knots. Night hauls, day hauls in italics.

Depth m	Jan.	Febr.	March	April	May	June	Oct.	Nov.
5.....	3	—	—	29	25	—	14	36
10.....	14	28	—	32	37	6	—	—
15.....	—	—	—	16	28	—	—	—
25.....	24	37	14	—	—	5	—	16
	—	—	—	—	—	—	—	—
50.....	82	6	13	6	13	13	12	22
	9	*3*		*1*			*2*	
100.....	39	38	—			13	6	
	—	*15*	—	*2*	*3*	—	*17*	
130.....	15	31	15	—	—	—	—	—
	17	*41*	—	*20*	—	—	—	—
180.....	38	38	—	—	—	13	14	—
	—	*29*	—	*11*	*8*	—	*15*	—
230.....	34	13	—	—	13	7	9	—
		41	—	*10*	*26*	*11*	*7*	—

is inferred that the figures give some information on the relative abundance of krill. In the Byfjord (Table 1) the volumes per 1 000 m³ varied between 13 and 41 ml, with one single figure of 82 ml in January. In a CB haul at 3 m level during the night of 19 November 1968 the volume was about 100 ml/1 000 m³.

Some IKMT hauls were made at varying times of day and night (Table 2). In January 1967 maximum in volume was observed at 50 m during the afternoon and evening, but after midnight the krill were evenly dispersed below 50 m. In February no krill were taken at 50 m or above during the day, the volume increasing from 100 m to 230 m. At dusk krill were taken from 25 m, increasing to a maximum volume in 150—200 m. In October the maximum was found in 100—200 m during the day, but at 10 m during the night. In February 1968 maximum was again below 200 m during the day, and at 10 m during the night, but in 50—230 m the krill were rather evenly distributed.

In the Hardangerfjord the volumes of krill in IKMT night hauls in 10—50 m usually were 7—30 ml/1 000 m³, but in April 1968, 83—104 ml/1 000 m³ were taken at 5 m level. In the Karmsund (Fig. 1) 167 ml/1 000 m³ were taken in a night haul at 5 m in November 1968.

None of the quantities taken indicate densities comparable with those induced by artificial light (Wiborg 1966).

Table 2. Volumes of krill and mysids in ml per 1 000 m³ in the Byfjord 1967 and 1968.

Year	Date	Hour	Depth, m							
			5	10	25	50	100	150	200	230
1967.....	6—7 Jan.	1630—1700	—	—	24	45	18	17	17	33
		2000—2100	—	—	13	82	27	—	31	34
		0020—0150	—	—	16	36	39	—	38	38
1967.....	6 Febr.	1306—1430	—	—	0	0	14	—	29	41
		1630—1835	—	—	11	6	26	31	38	13
1967.....	16 Oct.	1020—1230	—		—	2	17	—	15	7
		2115—2330	14		—	11	6	—	13	9
1968.....	5 Febr.	1020—1200	—	0.4	—	0.4	2.0	—	20	30
		2050—2330	7	37	—	18	23	—	25	21

RELATIVE COMPOSITION OF KRILL AND MYSIDS IN THE IKMT CATCHES

Nine species of krill have been identified in the catches, viz. *Meganyctiphanes norvegica* (M. Sars), *Thysanoessa inermis* (Krøyer), *T. raschii* (M. Sars), *T. longicaudata* (Krøyer), *Nyctiphanes couchii* (Bell), *Thysanopoda acutifrons* (Holt and Tattersall), *Nematoscelis megalops* (G. O. Sars), *Euphausia krohnii* (Brandt) and *Stylocheiron maximum* (Hansen). The last four species have been dealt with earlier (Wiborg 1968). In this paper the main emphasis will be laid on *M. norvegica, T. inermis* and *T. raschii,* both in number and volume dominating the catches.

The mysids, *Boreomysis arctica* (Krøyer), *B. megalops* (G. O. Sars), *Siriella norvegica* (G. O. Sars) and *Lophogaster typicus* (M. Sars) have been included in the counts used in Fig. 3, but otherwise not dealt with.

According to Jerde (1967) krill below a size of 13 mm are not caught quantitatively in a net with a mesh size of four mm. As will be shown later, this also seems to be the case with the three mm net used in the present investigation. Reservations must also be taken that the deeper hauls contain krill taken at upper levels. The composition of the samples may nevertheless indicate the relative abundance of the different species, especially during winter and spring when the smaller species have reached their adult size. In Fig. 3 are shown the relative numerical abundance of *T. raschii, T. inermis, M. norvegica,* and the group other krill and mysids (mainly *B. arctica* and *L. typicus*, in the Byfjord in 1967—1968.

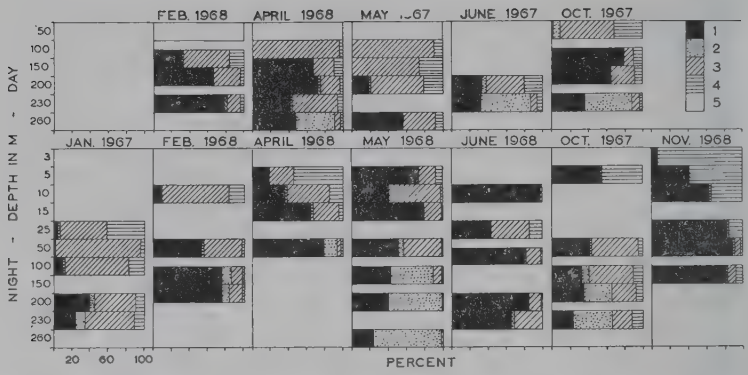


Fig. 3. Relative numerical importance of the most abundant species of krill and mysids in Isaacs-Kidd 3' pelagic trawl in the Byfjord in 1967—1969. 1) *Meganyctiphanes norvegica,* 2) Mysids, 3) *Thysanoessa inermis,* 4) *Thysanoessa raschii,* 5) hauls with no catch.

During the day, *T. inermis* and *T. raschii* dominate the uppermost hauls, in May also in 200 m. During the night conditions vary, sometimes with *T. raschii* dominating in the upper 5—10 m and *T. inermis* second, but *M. norvegica* dominates at 10—15 m in April—May, and at 5—10 m in May—June and October. In September 1967 (not figured), October 1967 and November 1968 only *T. raschii* and *M. norvegica* were taken in the upper 10 m during the night, *T. inermis* appearing at 25—50 m. This feature is in accordance with the observations of Lacroix (1961) in Canadian waters.

M. norvegica as a rule dominates below 150—200 m during the day. Mysids, mainly *B. norvegica,* sometimes also *L. typicus,* are occasionally rather numerous below 100—200 m, especially during the night, sometimes ascending to 10 m (April 1968).

In volume *M. norvegica* will nearly always dominate the samples because it is 10—15 times as big as *T. inermis* and *T. raschii.* More details about the vertical distribution will be given later in this paper.

THE KRILL SPECIES

MEGANYCTIPHANES NORVEGICA

Abundance

As the sampling did not include the entire water column from bottom to surface, the material is not very well suited to give information on the variation of the stock as a whole.

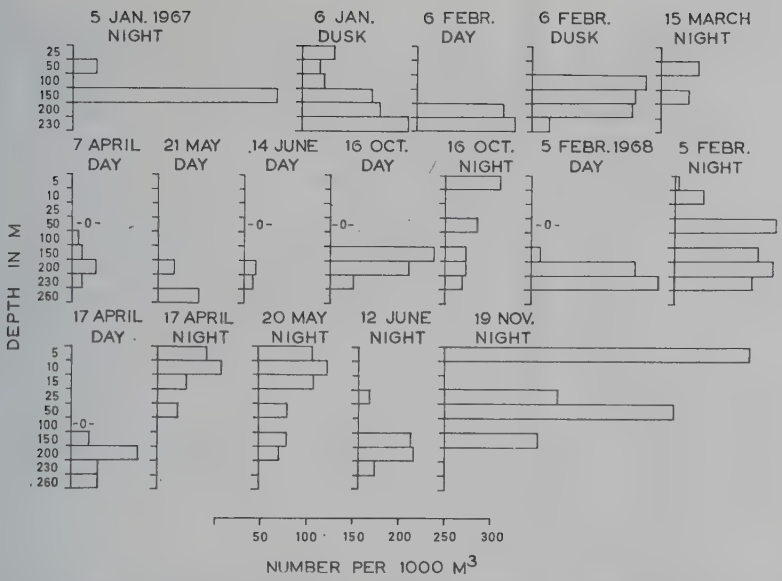


Fig. 4. Numbers of *Meganyctiphanes norvegica* per 1 000 m³ at different levels in the Byfjord in 1967—1968. —0—) no catch.

In Fig. 4 are given numbers per 1 000 m at various levels during day and night in the Byfjord in the period from January 1967 to November 1968. The figures were fairly high in January—February 1967, 125—220 specimens/1 000 m³ in the deeper hauls. In March—June numbers were low, 42 or less. In February 1968 the stock seemed to be of the same size as in February 1967, but with less reduction to April—June than in the year before. In June 1968 the new generation appeared as furciliae in the upper 10 m. In November the stock was possibly more abundant than in November 1967.

During January—June 1967 night hauls in the Hardangerfjord in 10—50 m yielded 20—55 specimens/1 000 m³. A day haul at 200 m in February 1967 at Røyrvik yielded 190 specimens/1 000 m³; in Karmsund a night haul at 4 m in November 1968 yielded 1 370 specimens/1 000 m³.

Vertical distribution and migration

As is evident from Fig. 3 and 4, *M. norvegica* in the Byfjord as a rule keeps below 100—150 m during the day, but may ascend to the surface at night. According to Einarsson (1945) and Mauchline (1960) larger

individuals as a rule stay deeper than the smaller ones. This was also observed in the Byfjord (Fig. 5). In February 1967 small individuals (less than 28 mm) during the day dominated at 200 m and 230 m. In the evening a few larger specimens appeared at 100 m. In 150—230 m large specimens constituted more than half the stock. In February 1968 distribution was similar, most of the larger individuals evidently staying below 200 m during the day. During the night a few large specimens were taken at 10 m, the proportion increasing to a maximum in 175—210 m. In April 1968 larger individuals (I-group) during the day were very scarce at 150 m and 220 m, but relatively abundant at 260 m. During the night this group was well represented even at 15 m. In October specimens larger than 30 mm appeared in increasing percentage from 100—150 m and downwards during the day. During the night only small *Meganyctiphanes* were taken at 5 m, but the proportion of those above 30 mm increased from 6 % in 25—75 m to 54 % in 220—260 m.

During February—June adult males stayed somewhat deeper than

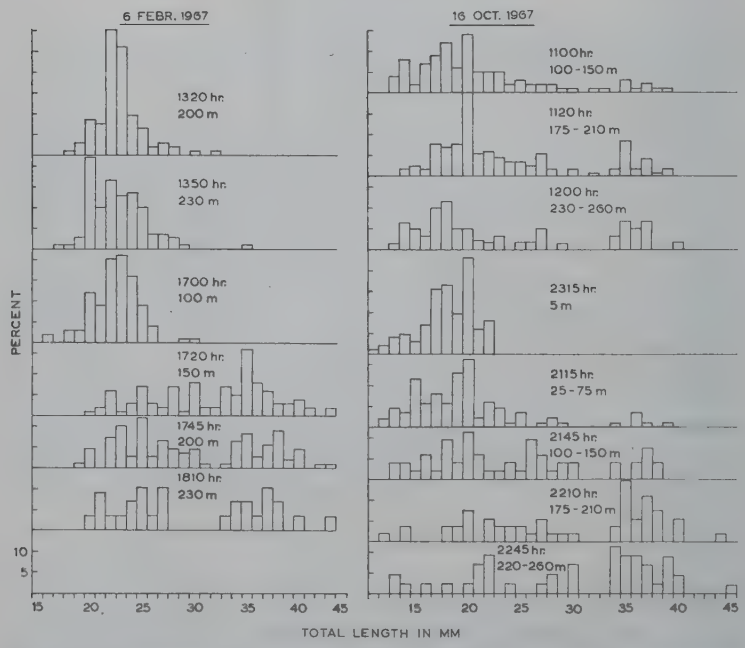
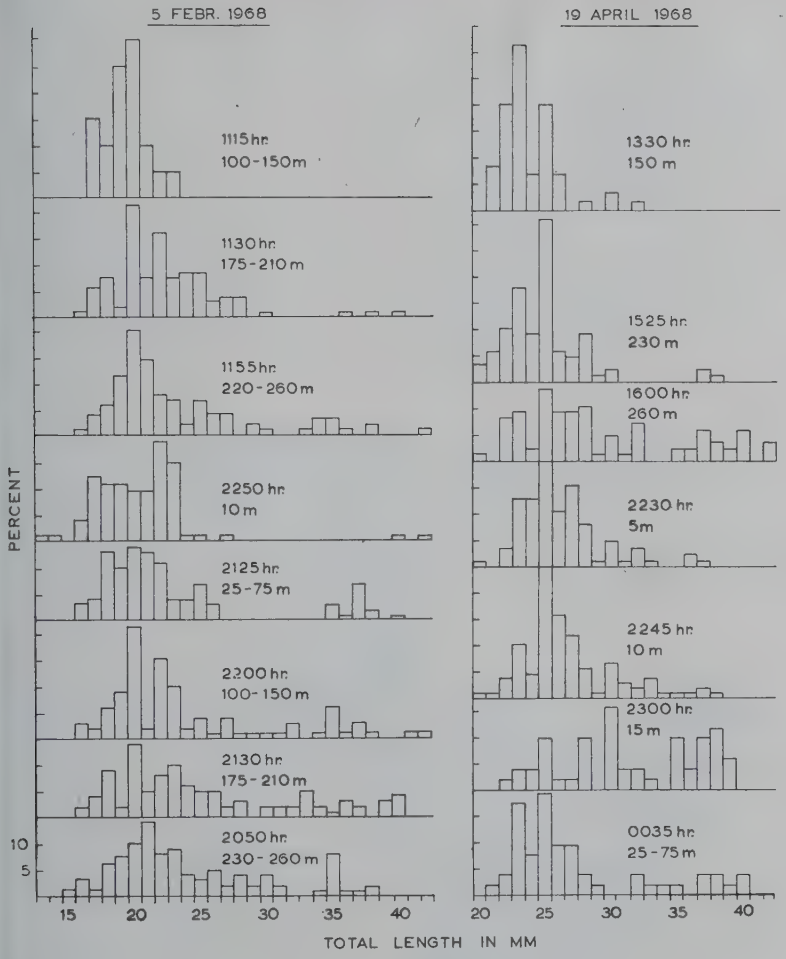


Fig. 5. Size distributions of *Meganyctiphanes norvegica* at different levels during day and night in the Byfjord in February and October 1967, and in February and April 1968.

Fig. 5. continued.



the females as indicated by the increase in the proportion of males with increasing depth (Table 4).

In samples taken with light and dipnet from a pier in the Hardangerfjord in November 1965 and January 1966 (Table 3) the proportion of larger individuals in November increased from midnight to a maximum in early morning. In January large individuals appeared already in the evening.

Table 3. Percentages of the various size groups of *Meganyctiphanes norvegica* taken with light and ketcher in the Hardangerfjord area in 1965—1966.

Year	Date	Hour	26 mm	27—30 mm	33—40 mm	25 mm	26—36 mm
1965.....	25 Nov.	2100	100	0	0		
		2300	98	2	0		
	26 Nov.	0300	92	8	0		
		0500	66	24	10		
		0745	58	20	20		
1966.....	14 Jan.	1830				97	3
		2300				90	10
	15 Jan.	0400				73	27

Growth

In the Byfjord (Fig. 6) two size groups were generally found, the O-group and I-group and I-group. In November 1966 the O-group measured 14—27 mm, mean 19 mm. A few I-group specimens measured 29—34 mm. In January 1967 the O-group ranged from 19 mm to 30 mm, mean 24 mm, increasing in June to 28—33 mm. The I-group had

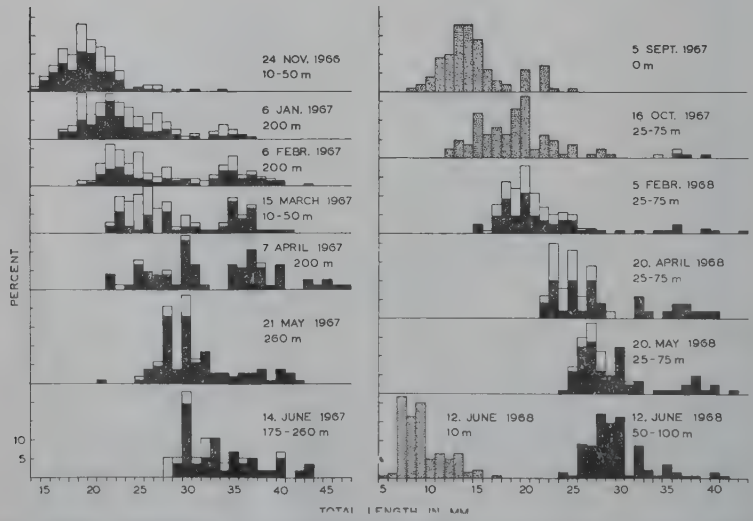


Fig. 6. Size distributions of *Meganyctiphanes norvegica* in the Byfjord (selected hauls) in 1967—1968. Black) females, white) males.

a less pronounced increase, with the peak moving from 34 mm in January to 38—39 mm in June. Individuals probably belonging to the II-group, 43—47 mm, appeared in February and April 1967.

In September 1967 the new 0-group measured 8—25 mm with a peak at 13—14 mm. From October 1967 to June 1968 the development was similar to that of the preceeding season, but in February the 0-group individuals were smaller than the 0-group one year before. In June 1968 the brood of the year appeared as furciliae and adolescents, measuring 5—15 mm.

In the Hardangerfjord (Fig. 7) the variations in size distribution from November 1966 to June 1967 were similar to those in the Byfjord, but the 0-group individuals were slightly larger. This may be due to local growth conditions which may vary from year to year.

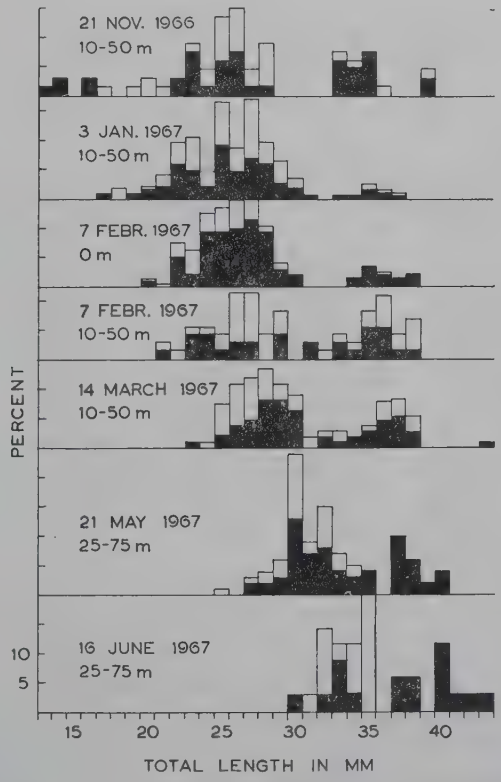


Fig. 7. Size distributions of *Meganyctiphanes norvegica* in the Hardangerfjord in 1967. Black) females, white) males.

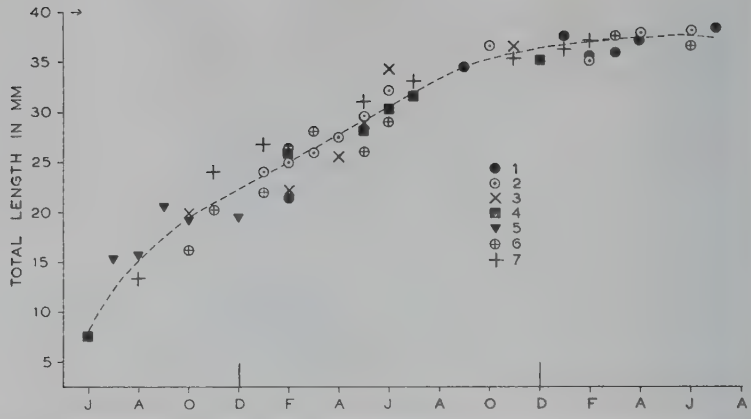


Fig. 8. Mean length of various year classes of *Meganyctiphanes norvegica* as 0-group and I-group in the Byfjord (1—5) and in the Hardangerfjord (6—7) in various months of the year. 1 and 6) 1965, 2 and 7) 1966, 3) 1967, 4) 1968, 5) 1969.

In Fig. 8 the mean length of the 1965—1969 year classes of *M. norvegica* has been plotted, using all the data available for the Hardangerfjord including data from Wiborg (1966). Variations in growth are most evident during the first year. The length increases from 7.5 mm in June to about 22 mm in December, further to 27 mm in April, and to 30—34 mm in June. During the second year of life the growth rate seems to decrease, the *Meganyctiphanes* reaching a mean length of 37—38 mm two years old. Individuals, 43—47 mm in length, taken in April 1967 (Fig. 6) are possibly nearly three years old.

It is difficult to find retardation of growth during the autumn and winter as was stated by Mauchline (1960). This may be due to a long spawning period. The growth rate is similar to that found by Paulsen (1926) for *M. norvegica* in the Skagerrak.

Maturity, sex proportions and spawning

Males have been characterized as mature when spermatophores could be clearly seen in the spermatheca and females when the thelycum could be distinguished. Percentages of mature individuals, of males, and of females with spermatozoa in the thelycum (fertilized) in the Byfjord in 1967—1968 are given in Table 4.

Table 4. *Meganyctiphanes norvegica*. Percentages of: 1) mature individuals in the samples, 2) males of the mature animals, 3) females with attached spermatophores of all the females in the Byfjord in January—June 1967 and February—June 1968. IKMT hauls.

Year	Date	Day or night	Depth m	1. mature %	2. males %	3. females with spmtf. %
1967.....	6 Jan.	night	25	0		0
		»	50	45	about 50	0
		»	100	60		0
		»	200	33		0
		»	230	52		0
	6 Febr.	night	100	56		11
		»	150	92	about 50	55
		»	200	90		47
	15 March	night	10— 50	100	47	95
		»	150	100	73	100
	7 April	night	100	100	0	100
		»	150	100	6	86
		»	200	100	7	85
		»	230	100	9	86
	21 May	day	200	100	10	40
		»	230	100	10	73
	14 June	night	175—210	100	25	16
1968.....	5 Febr.	night	10	31	—	0
		»	25— 75	40	42	(33)
		»	100—150	50	53	(33)
		»	230—260	55	49	(31)
	19 April	night	4	100	5	91
		»	10	100	12	99
		»	15	100	0	100
		»	25— 75	84	30	78
	20 May	night	4	100	1	100
		»	10	100	0	100
		»	15	100	0	100
		»	25— 75	100	21	100
		»	100—150	100	50	100
		»	200	100	63	100
		»	260	100	79	100
	12 June	night*)	10	100	0	100
		»	25	100	0	100
		»	50—100	100	0	100
		»	200	100	33	97
		»	230	100	33	100

*) The new 0-group excluded.

No mature individuals were found in November 1966, probably because no deep hauls were taken. In January the percentage of mature individuals increased from 0 at 25 m to 33—60 below 50 m, in February to 56—90 and fertilized females were observed. In March the whole stock was mature, and nearly all females were fertilized. In April the proportion of fertilized females was still high, but decreased throughout May to a low level in June.

Males and females were nearly equal in number from November 1966 to the middle of March 1967. In April the percentage of males decreased to below 10, remaining low in May and June. In 1968 the proportions of mature individuals and of fertilized females were lower in February than one year before, but had increased considerably until April. The percentages of fertilized females remained high in May and June. Males decreased very much in percentage from February to April and were scarce in the upper hauls in May, but the percentage increased to 79 at 260 m. In samples taken in 1969 the percentage of fertilized females

Table 5. *Meganyctiphanes norvegica*. Percentages of: 1) mature individuals in the samples, 2) males of the mature animals, 3) females with attached spermatophores of all the females in the Hardangerfjord, January—June 1967 and February—April 1968. IKMT night hauls. Italics: Catches with light and ketcher.

Year	Date	Depth m	1. mature %	2. males %	3. females with spmtf. %
1967.....	3 Jan.	10— 50	70	42	7
		20	67	61	0
	4 Jan.	40	80	65	25
		60	80	72	13
	7 Febr.	0	90	26	46
		10— 50	85	56	42
		150	98	33	58
	14 March	10— 50	100	46	100
		150	100	39	100
	21 May	25— 75	100	32	100
	16 June	25— 50	100	50	100
		75—100	100	89	100
1968.....	12 Febr.	10	74	47	46
		25— 75	91	68	43
		100—150	(93)	(20)	(33)
	23 Febr.	*0*	*100*	*34*	*100*
	27 March	*0*	*100*	*14*	*100*
	18 April	*0*	*100*	*0*	*100*
		4— 15	100	18	100

was 60—80 in June and dropped to 20 in the middle of July. As was found earlier (Wiborg 1966), larger females were fertilized before the smaller ones. In February 1967, 70 % of the females above 31 mm were fertilized, of those below 31 mm only 30 %. In February 1968 the corresponding figures were 75 % and 24 %.

In the Hardangerfjord (Table 5) 67—80 % of the individuals were mature in January 1967, increasing to 85—90 % in February and to 100 % from the middle of March. The proportion of males was relatively high in January—June 1967; minimum 26 % in a sample taken with ketcher and light in February. Fertilized females appeared in January, the percentage increasing with increasing depth. In February about half of the females, in March all, were fertilized.

In 1968 nearly all individuals were mature in the middle of February and half of the females fertilized. On February 23 individuals lured with light were all mature, the females fertilized. In March—April the percentage of males was reduced to 0—18. In 1967 the females fertilized in January measured 34—42 mm (I- and II-group), in February 87 % were above 31 mm.

Mortality

As already mentioned, the stock as a whole is considerably reduced from February to March, and the proportion of males decreased from March to April both in the Byfjord and the Hardangerfjord. It is also expected that older individuals (I- and II-group) would die at a higher rate during spring than the 0-group. The proportion of I-group to 0-group males and females in the Byfjord in 1967—1968 is shown in Table 6.

During February—June old males were less frequent than old females, in some samples entirely absent. In 1967 the percentage of old females in January was about 25, of males 20. In February old females were mainly taken below 150 m during the night. In March these females were relatively frequent at higher levels, males at 150 m. In April—June old males were scarce or absent, and the percentage of old females was also reduced.

In October the 0-group dominated during the day and above 175 m during the night. At and below 175 m the I-group constituted more than 50 %.

In 1968 old males were poorly represented, only taken in deep hauls in February. Old females were also generally scarce, indicating a poorer survival than in the spring of 1967. In the Hardangerfjord (Table 7) conditions in 1967 varied very much in the different parts of

Table 6. *Meganyctiphanes norvegica:* Proportions of I-and II-group to 0-group of males and females in the Byfjord, January 1967 to May 1968. IKMT-hauls. ÷) no males present.

Year	Date	Day or night	Depth m	I-II gr. / 0-gr. males %	I-II gr. / 0-gr. females %
1967.....	5 Jan.	night	10— 50	7	20
		»	150	14	26
	6 Jan.	»	100	6	24
		»	200	20	24
		»	230	32	32
	6 Febr.	day	240	0	2
		»	100	÷	0
		»	150	38	77
		»	200	26	43
	15 March	night	10— 50	8	53
		»	150	33	55
	7 April	day	150	0	18
		»	200	20	49
		»	230	0	60
	21 May	day	200	0	0
		»	230	0	19
	14 June	»	175—210	7	26
	16 Oct.	»	100—150		13
		»	175—210		21
		»	230—260		25
		night	5		0
		»	25— 75		8
		»	100—150		27
		»	175—210		54
		»	230—260		61
1968.....	5 Febr.	day	175—210	0	3
		»	230—260	9	9
		night	10	0	8
		»	25— 75	0	28
		»	175—210	14	38
		»	230—260	28	34
	17 April	day	150	÷	0
		»	200	0	2
		»	230	0	4
		»	260	0	36
	19 April	night	4	0	4
		»	10	0	5
		»	15	0	40
		»	25— 75	0	27
	20 May	night	4	÷	6
		»	10	÷	3
		»	15	÷	15
		»	25— 75	÷	17

Table 6(cont.). *Meganyctiphanes norvegica:* Proportions of I-and II-group to 0-group of males and females in the Byfjord, January 1967 to May 1968. IKMT-hauls. ÷) no males present.

Year	Date	Day or night	Depth m	I-II gr. / 0-gr. males %	I-II gr. / 0-gr. females %
	10 May	»	100—150	0	24
		»	200	0	67
1968	12 June	night	10	÷	0
		»	25	÷	10
		»	50—100	÷	4
		»	200	0	9
		»	230	0	0

the fjord, but the proportion of old males generally decreased considerably after March. The impression is also that the stock as a whole was heavily reduced after spawning. Occasionally old females dominate catches taken with dip net and light, in February 1968 constituting up to 95 %. Similar observations have been made earlier (Wiborg 1966).

Table 7. *Meganyctiphanes norvegica:* Proportions of I- and II-group to 0-group of males and females in the Hardangerfjord January 1967 — April 1968. IKMT night hauls. At 0 m, catches with light and ketcher. ÷) no males present.

Year	Date	Depth m	I-II gr. / 0-gr. males %	I-II gr. / 0-gr. females %
1967.....	3 Jan.	10— 50	55	57
	7 Febr.	0	1	15
		10— 50	37	42
		150	44	55
	14 March	10— 50	39	41
		10— 50	27	38
	21 May	25— 75	0	40
	16 June	150	8	27
1968.....	12 Febr.	10	0	31
		25— 75	50	50
	18 Febr.	0	0	95
	23 Febr.	0	23	69
	27 March	0	21	33
		0	8	21
	18 April	0	÷	10
		4— 15	0	20

Conclusions

In the investigated area *M. norvegica* was seldom taken in densities higher than 150 specimens/1 000 m³, with a single exception of 1 170 specimens/1 000 m³. However, dense agregations at the surface have been induced with artificial light.

During the day *M. norvegica* keeps below 150 m with maximum concentration at 200—260 m or deeper. During the night the population migrates towards the upper layers, sometimes close to the surface. A certain layering was observed, 0-group individuals in the top layer, older individuals successively deeper. Some of the I-group males stay in deeper water both during day and night. This pattern of vertical migration is similar to that described by Einarsson (1945) and Mauchline (1960, 1969). Occasionally older individuals arrived at the surface later in the night or early morning. Surface swarms of *M. norvegica*, attracted by artificial light in February—March, sometimes consisted mainly of 0-group females. A similar segregation of I-group individuals was observed by Aitken (1960, quoted by Mauchline 1969).

The growth of *M. norvegica* was comparable with that in the Skagerrak (Paulsen 1926). Hatched in April—May, the 0-group attains a length of 22 mm in December, 27 mm in April, and 30—34 mm as I-group in May—June. During the second year the growth decreases, the animals in May—June measuring about 38 mm. Individuals surviving for one more year measure 43—47 mm next April.

Maturing and copulation starts in January, the I-group females being fertilized first. All individuals are usually mature and all females fertilized in the middle of March. Spawning starts in March—April, sometimes continuing throughout June.

As was found by Mauchline (1960), there is a high mortality in the males during and after the transference of spermatophores in March—April and also a higher mortality in the I-group than in the 0-group in March—May. Because of the vertical segregation of the different size groups in the water mass, it is difficult to give exact figures of the mortality. In the Byfjord the survival of the I-group in the spring was definitely better in 1967 than in 1968.

THYSANOESSA INERMIS

Abundance and vertical distribution

In night hauls in the Byfjord 395 specimens/1 000 m³ were taken in November 1966, 1 500—3 600 specimens/1 000 m³ at 40—50 m level in January—February 1967 (Table 8). During April—June and in October

Table 8. *Thysanoessa inermis*. Number per 1 000 m³ in hauls with 3' IKMT and Clarke—Bumpus plankton sampler (CB) in the Byfjord in 1967—1968.

Year	Date	Day or night	Depth m	Number of *T.inermis*	Number of *T.inermis* at other levels
1966.....	24 Nov.	night	10— 50	395	
1967.....	5 Jan.	»	10— 50	580	
	6 Jan.	»	50	3 600	52—215
	6 Febr.	day	100	290	4—125
	9 Febr.	night	10— 50	94	
	9 Febr.	»	10 (CB)	350	
	9 Febr.	»	40 (CB)	1 560	
	15 March	»	10— 50	63	
	7 April	day	150	19	5— 9
	21 May	»	260	63	54
	14 June	»	175—210	63	10
	16 Oct.	night	25— 75	38	5— 25
1968.....	5 Febr.	»	5	27	
	5 Febr.	»	10	1 500	
	5 Febr.	»	10 (CB)	4 000	22—112
	17 April	»	10	32	7— 30
	20 May	»	25— 75	26	3— 21
	12 June	»	100	9	1— 7
	19 Nov.	»	50	35	0— 7

figures were low. High figures, 4 000 specimens/1 000 m³, were again obtained at 10 m level in February 1968.

In the Hardangerfjord *T. inermis* was taken in low numbers, maximum 125/1 000 m³.

In Karmsund an IKMT haul at 5 m in November 1968 yielded about 1 100 specimens/1 000 m³.

The irregular variation in abundance indicates an extensive degree of shoaling. Large numbers were only taken in night hauls and even then, only at one single level. The greater number usually taken in CB sampler as compared with the IKMT hauls, indicates that the smaller specimens pass through the meshes of the IKMT. There seems to have been a general decrease in the stock after February, both in 1967 and 1968. During the day *T. inermis* was usually most abundant at 100—200 m, during the night at 10—50 m.

Size distribution

In the Byfjord there was a major peak in the size distribution of *T. inermis* at 15 mm from November 1966 to the middle of March 1967

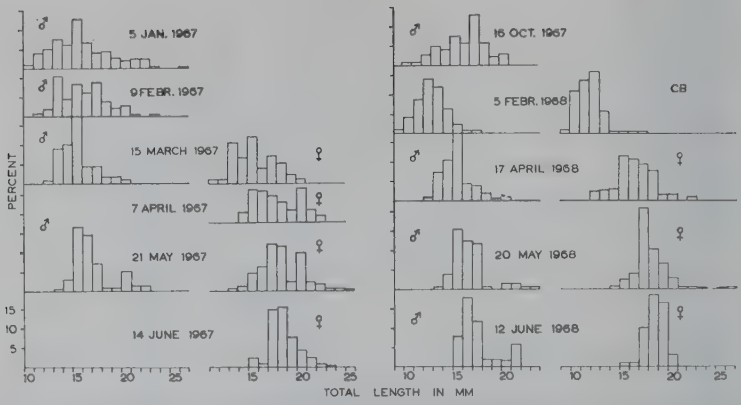


Fig. 9. Size distributions of *Thysanoessa inermis* in the Byfjord in 1967—1968. CB) from samples taken with Clarke—Bumpus plankton sampler.

(Fig. 9). In the March—June samples males and females were measured separately. Females were somewhat larger than the males with the peaks in May at 17 mm and 15 mm respectively. In both sexes there is a second peak at 20 mm, also observed in the females in April. In June the females were slightly larger than in May. In all samples taken in October 1967 there was a peak at 17 mm, in February 1968 at 12 mm. Comparing samples taken at the same level with IKMT and CB, it is evident that more small individuals are caught in the CB indicating escapement of the smaller sizes through the meshes of the IKMT.

In May 1968 the females passed the males in size, with peaks in June at 18 mm and 16 mm respectively.

T. inermis seems to be mainly annual in the Byfjord as was also found for the Hardangerfjord (Wiborg 1966). Individuals, 24—26 mm, taken in January—February 1967 may belong to the I-group.

Spawning and mortality

In the middle of March 1967 males constituted 35—40 % of the stock. Of the males 11 % carried spermatophores. At the beginning of April males were reduced to 7—8 %, indicating a heavy mortality, whereas all females carried spermatophores. In May males were again relatively more frequent, 4—48 %, possibly related to an increased mortality in females after spawning (Mauchline 1966). In June 58 % of the females carried spermatophores, and the males constituted 17 -20 %, but the stock was very small. Eggs and nauplii of *Thysanoessa*

sp. were found in vertical Juday net hauls from the middle of March. Maximum of spawning probably occurred in early April. In 1968 males constituted 18—24 % in April, 34 % in May. Nearly all the females carried spermatophores both in April and May except from hauls at 200—230 m where 19 % were not fertilized.

In the Hardangerfjord the samples were too scarce to give sufficient information of the spawning.

Occurrence of the two-spined form of T. inermis

According to Hansen (1911, 1916, quoted by Jones, Forsyth and Cooper 1967) *T. inermis* from the Pacific Ocean has two dorsal spines, on respectively the fifth and sixth abdominal sediment; in the Atlantic generally only one, on the sixth segment. Recently, Jones *et al.* (1967) found the two-spined form in the North Sea occurring in about three percent of the individuals investigated.

During the present investigation the two-spined form has also been found in the Hardangerfjord, in the Byfjord and in the Sognefjord (Fig. 1). The frequency was from 1 to 3 percent, the size of the individuals 11—20 mm.

One specimen has also been recorded in samples taken at station M at 66°N, 02°E.

The finding of the two-spined form in the coastal areas of Western Norway links very well with the occurrence in the North Sea.

THYSANOESSA RASCHII

According to Mauchline (1969) *T. raschii* is a neritic species widely distributed in the northern oceans and also found along the coast of Norway. Einarsson (1945) states that it prefers sheltered fjords, but occurs also in coastal areas.

Abundance and vertical distribution

During the present investigation *T. raschii* was taken regularly in the Byfjord (Table 9), but in numbers second to *T. inermis* except in February 1967 and November 1968. In 1967 maximum numbers were taken in January and February (3 500 specimens/1 000 m^3), in 1968 in February and November. Figures then amounted up to 700 and 5 000 specimens/ 1 000 m^3 respectively. In the Hardangerfjord *T. raschii* was always very scarce, maximum 2—3 specimens/1 000 m^3. In Karmsund (Fig. 1) 85 and 230 specimens/1 000 m^3 were taken in May and November 1968 respectively.

Table 9. *Thysanoessa raschii*. Number per 1 000 m³ in hauls with 3' IKMT and Clarke—Bumpus plankton sampler (CB) in the Byfjord in 1967—1968.

Year	Date	Day or night	Depth m	Number of *T.raschii*	Number of *T.raschii* at other levels
1966.....	24 Nov.	night	10— 50	230	
1967.....	5 Jan.	»	10— 50	440	
	6 Jan.	»	25	163	
			50	150	1—40
	6 Febr.	day	100	147	6—26
	9 Febr.	night	10— 50	68	
			10 (CB)	3 500	
			40 (CB)	100	
	15 March	night	10— 50	2	1
	7 April	day	150	9	1— 7
	21 May	»	200	19	6
	14 June	»	175—210	19	3
	16 Oct.	night	5	100	3— 9
1968.....	5 Febr.	»	5	165	
			10	315	3— 7
	6 Febr.	night	10 (CB)	720	
	17 April	»	5	125	0— 3
	20 May	»	5	9	1— 6
	12 June	»	25	4	0— 1
	19 Nov.	»	5	365	10—22
			25	22	
			3 (CB)	5 000	
			8 (CB)	730	

During the night *T. raschii* was nearly always most abundant in the upper 5—10 m, and in November 1968 it was more numerous at 3 m than at 8 m. During the day maximum number was usually taken at 100—150 m.

Size distribution

Size distributions (Fig. 10) are similar to those of *T. inermis*, but there are some differences. From November 1966 to February 1967 there were peaks at 13 mm and 15 mm. Few individuals were caught in March. In April males and females had peaks at 15 mm; in May the females were larger (18 mm) than the males (15—16 mm). In June the peaks were at 17 mm and 20 mm respectively. From September 1967 to February 1968 the peak was mainly at 12—13 mm. Figures from catches with IKMT and CB samplers 1968 are compared, showing the escapement of smaller individuals through the meshes of the IKMT.

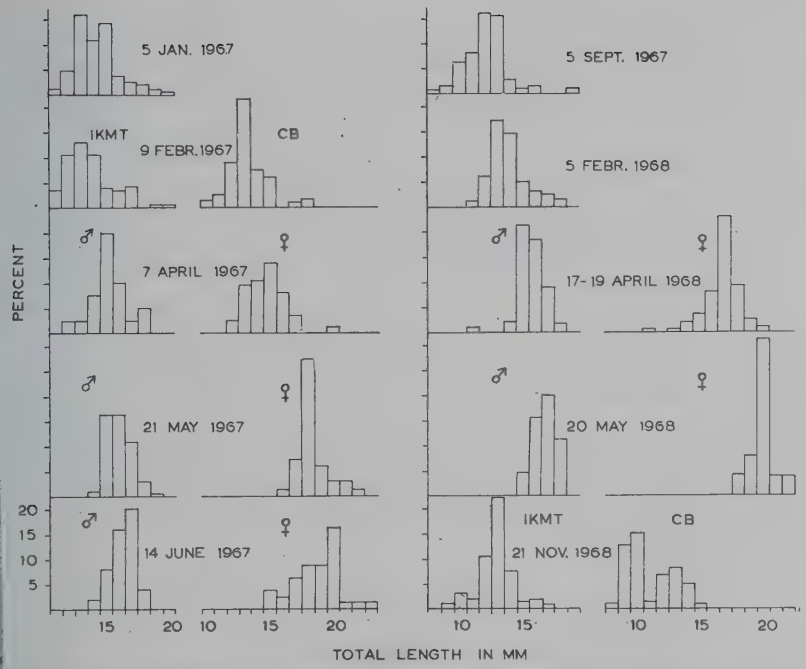


Fig. 10. Size distributions of *Thysanoessa raschii* in the Byfjord in 1967—1968. CB) from samples taken with Clarke—Bumpus plankton sampler.

T. raschii was slightly larger in April and May 1968 than in the same months the year before. In November two peaks are indicated, at 10 mm and 13 mm, and escapement of smaller individuals from the IKMT hauls is again apparent.

Spawning

In March 1967 the few individuals taken were immature. At the beginning of April 76 % of the females carried spermatophores. Males constituted 20 % of the stock. In May males were more numerous than females, (70 %), probably indicating a high mortality in the females after spawning as was found by MAUCHLINE (1960, 1969) for *M. norvegica*. In June 58 % of the females carried spermatophores, and the percentage of males had increased to 40.

In 1968 all females were fertilized in the middle of April and the male percentage was 33, increasing to 63 in May.

In Karmsund the same picture was observed in May 1968, most of the females fertilized and males dominating.

Conclusion

The preference of *T. raschii* for the upper 5—10 m layer during the night has already been mentioned. This fact in addition to the mesh size of the trawl may possibly lead to an underestimate of the numerical importance of this species. This is clearly evident in the figures for 9 February 1967 (Table 9). The size distributions are on the whole more uniform than in *T. inermis*, usually with one main peak. In May and June the mean lengths are greater than those of *T. inermis*, but the survival of individuals beyond one year seems to be insignificant, indicated by a few individuals of 22—23 mm in May—June.

Spawning occurs from April to June with maximum in the middle of April and, to judge from lack of mature individuals in March, somewhat later than in *T. inermis*. The same difference was also observed in the Barents Sea (Zelikman 1958). The two peaks in the size distributions in January—February 1967 and in November 1968 may indicate a spawning period with two maxima for the years 1966 and 1968 while there seems to have been only one main period in 1967. Similar year to year differences are reported by Mauchline (1966).

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ON ACOUSTIC IDENTIFICATION, SIZING AND ABUNDANCE ESTIMATION OF FISH

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ABSTRACT

Midttun, L. and Nakken, O. 1971. On acoustic identification, sizing and abundance estimation of fish. *FiskDir. Skr. Ser. HavUnders.*, *16*: 36—48.

A method using the fish angle (i.e. the change in target strength with fish aspect) for identification purposes is described. Significant differences in fish angle between cod and coalfish have been observed at sea. The effect of fish angle on the sampling volume of an echosounder is discussed, and it is shown that the sampling volume decreases with decreasing fish angle. A method for abundance estimation applying an echo integrator is described and discussed.

INTRODUCTION

When fish targets are recorded with an echo sounder, three main questions arise:

What kind of fish is it?

What is the size of the fish?

What is the fish density, i.e. number of fish per unit volume water or per unit area?

Fish recordings have so far been idenfified by capture or underwater photography (Parrish and Craig 1969) and also, to some extent, by recognition of typical traces on the recording paper. While the two first methods are time consuming, the third depends on the experience and skill of the observer, and there are no general rules which can be applied for an acoustic identification.

Information on the size of the recorded fish can be obtained from knowledge of target strenght which may be found by an analysis of the received echo signals (Cushing 1968, Craig and Forbes 1969).

The problem concerning the fish density can be regarded as consisting of two parts. Firstly, there is the question of counting or measuring the numbers of fish detected, and secondly, that of finding the sampling volume.

The present paper aims at a technique of direct acoustic identification and sizing of the recorded fish. Further it describes a method for abundance estimation by the application of an echo integrator.

IDENTIFICATION AND SIZING

THE DETECTION SECTOR ANGLE, φ

When the sounding ship passes over an individual target, the sector angle, φ, within which the target is detected, can be determined by the number of echoes received from it during successive transmissions (Fig. 1).

$$\varphi = 2 \; arctg \; \frac{v \; (n+1)}{2 \; D \cdot p} \qquad (1)$$

v is the speed of the ship in cm/sec., n is the number of echoes received from the target, D is the depth of the target in cm and p is the repetition rate of the sounder in number of transmissions per sec.

If the target is a sphere and is passed through a circular beam a number of times at different distances from the acoustic axis, the frequency distribution of φ will be as shown in Fig. 4 D. The maximum value of φ, (φ_{max}), occurs when the target passes through the beam center. The value of φ_{max} depends on the directivity of the transducer and the target strength.

Fish targets however, do not reflect sound as does a sphere. The target strength of a fish varies with its orientation relative to the acoustic axis (Midttun and Hoff 1962, Haslett 1962 and 1965, Love 1969). The dorsal-lateral aspect target strength may be as much as 20 db higher than the head-tail aspect target strength. Therefore the target strength of an «ideal» fish can schematically be presented in a three-dimensional diagram as shown in Fig. 2.

Below, an attempt has been made to determine the frequency distribution of the detection sector angle φ when the «ideal» fish passes through a circular beam with different horizontal orientations and at different distances from the acoustic axis. The maximum target strength of the fish is assumed to be equal to that of the above mentioned sphere.

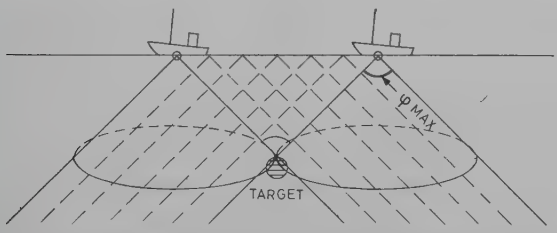

Fig. 1. Schematic picture of a transducer passing a target.

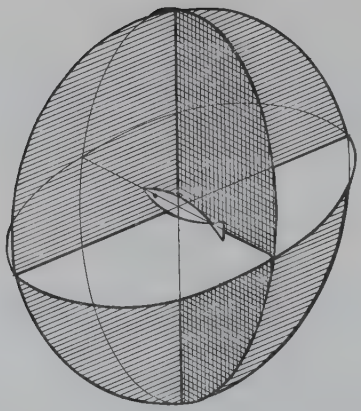

Fig. 2. Target strength pattern for an «ideal» fish target.

The maximum angle, φ_{max}, will occur when the fish passes through the center of the beam and is orientated with its long axis at a right angle to the course line. Then φ_{max} is equal to that of the sphere above.

The angle φ of a fish passing through the beam center with its long axis parallel to the course line will be smaller due to the rapid decrease in target strength (Fig. 2). This value of φ is called the fish angle, φ_f.

Thus, the area within which the vertically «looking» circular transducer can «see» the «ideal» fish, is formed approximately as an ellipse (Fig. 3), of which the axes are given by

$$a = 2\ D\ tg\ \frac{\varphi_{max}}{2} \text{ and } b = 2\ D\ tg\ \frac{\varphi_f}{2} \qquad (2)$$

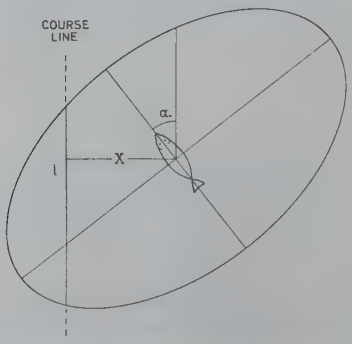

Fig. 3. Schematic presentation of the detection area of an «ideal» fish.

The detection sector angle φ can be written

$$l = 2\,D\,tg\,\frac{\varphi}{2} \tag{3}$$

where l is the length of an arbitrarily chord of the ellipse. In order to eliminate the depth D, l is expressed in parts of the long axis, a.

$$\frac{l}{a} = \frac{tg\,\frac{\varphi}{2}}{tg\,\frac{\varphi_{max}}{2}} \tag{4}$$

For practical applications (2) and (4) can be written

$$\frac{b}{a} = \frac{\varphi_f}{\varphi_{max}} \text{ and } \frac{l}{a} = \frac{\varphi}{\varphi_{max}} \tag{5}$$

The frequency distribution of φ can be expressed in terms of φ/φ_{max} or l/a. l is a function of α and X, where α is the angle between the long axis of the fish and the course line, and X is the horizontal component of the distance from the course line to the fish (Fig. 3). If the transducer is considered origin and the course line the y — *axis*, the following equation for the ellipse is obtained:

$$\frac{((x-X)\,cos\,\alpha - y\,sin\,\alpha)^2}{a^2} + \frac{(y\,cos\,\alpha + (x-X)\,sin\,\alpha)^2}{b^2} = 1$$

and

$$l = y_1 - y_2 \text{ for } x = 0 \tag{6}$$

This gives

$$\frac{l}{a} = \frac{\left(1 + \left(\frac{b^2}{a^2} - 1\right) sin^2\,\alpha - \frac{X^2}{a^2}\right)^{1/2}}{\frac{a}{b}\,cos^2\,\alpha + \frac{b}{a}\,sin^2\,\alpha} \tag{7}$$

Table 1. l/a as a function of $\frac{X}{a}$ and α for $b/a = 1/8$, $b/a = 1/4$ and $b/a = 1/2$.

$\frac{b}{a} = \frac{1}{8}$

	$\frac{X}{a}$								
α	0.1	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9
0.....	0.124	0.122	0.119	0.115	0.108	0.100	0.089	0.075	0.054
10.....	0.126	0.124	0.121	0.116	0.109	0.101	0.089	0.074	0.052
20.....	0.132	0.130	0.126	0.120	0.113	0.102	0.089	0.070	0.039
30.....	0.143	0.140	0.135	0.128	0.118	0.104	0.085	0.056	
40.....	0.161	0.157	0.149	0.139	0.123	0.102	0.068		
50.....	0.190	0.183	0.171	0.152	0.123	0.074			
60.....	0.240	0.225	0.198	0.152	0.052				
70.....	0.332	0.288	0.193						
80.....	0.518	0.201							
90.....	0.600								

$\frac{b}{a} = \frac{1}{4}$

	$\frac{X}{a}$								
α	0.1	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9
0.....	0.249	0.245	0.238	0.229	0.217	0.200	0.179	0.150	0.109
10.....	0.252	0.248	0.242	0.232	0.219	0.201	0.179	0.148	0.103
20.....	0.263	0.259	0.251	0.240	0.225	0.204	0.178	0.140	0.080
30.....	0.284	0.278	0.268	0.254	0.234	0.208	0.171	0.116	
40.....	0.317	0.309	0.295	0.275	0.246	0.205	0.143		
50.....	0.369	0.356	0.333	0.299	0.248	0.167			
60.....	0.451	0.427	0.383	0.312	0.182				
70.....	0.585	0.528	0.416	0.160					
80.....	0.783	0.621	0.076						
90.....	0.917	0.600							

$\frac{b}{a} = \frac{1}{2}$

	$\frac{X}{a}$								
α	0.1	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9
0.....	0.497	0.490	0.477	0.458	0.433	0.400	0.357	0.300	0.218
10.....	0.503	0.495	0.482	0.463	0.436	0.402	0.357	0.297	0.209
20.....	0.521	0.512	0.497	0.475	0.446	0.407	0.356	0.286	0.175
30.....	0.551	0.541	0.523	0.497	0.462	0.414	0.349	0.256	0.031
40.....	0.598	0.584	0.561	0.528	0.481	0.416	0.324	0.162	
50.....	0.662	0.644	0.612	0.565	0.497	0.399	0.236		
60.....	0.747	0.721	0.674	0.602	0.495	0.318			
70.....	0.848	0.808	0.737	0.624	0.439				
80.....	0.940	0.885	0.784	0.615	0.276				
90.....	0.980	0.917	0.800	0.600	0.000				

Table 1 shows l/a as a function of α and $\frac{X}{a}$ for three values of b/a. Frequency distributions of l/a are obtained from these tables and shown in Fig. 4. The distributions have marked peaks when l equals b or φ equals φ_f. Consequently, the fish angle, φ_f, can be found when φ_{max} is known. In Table 2 are listed frequency distributions of φ/φ_{max} for different values of φ_f/φ_{max}.

When all the fish recorded have the same fish angle, φ_f, and are distributed at random in horizontal orientation and distance from the acoustic axis, the distribution of φ/φ_{max} will be one of the horizontal distributions of Table 2. If however, there is a variation in fish angle, then the distribution of φ/φ_{max} can be considered as a sum of horizontal distributions in Table 2. Let n_1 be the number of observed φ_1 values, n_2 the number of observed φ_2 values and so on, and let further x_1 be the number of fish with $\varphi_f = \varphi_2$, x_1 the number of fish with $\varphi_f = \varphi_1$ and so on, then, the following set of equations is deduced

$$\begin{aligned}
a_{11}x_1 + a_{12}x_2 + a_{13}x_3 + \ldots\ldots\ldots\ldots + a_{110}x_{10} &= n_1 \\
a_{21}x_1 + a_{22}x_2 + a_{23}x_3 + \ldots\ldots\ldots\ldots + a_{210}x_{10} &= n_2 \\
\cdot \quad\quad \cdot \quad\quad \cdot \quad\quad\quad\quad\quad\quad \cdot \quad\quad \cdot & \\
\cdot \quad\quad \cdot \quad\quad \cdot \quad\quad\quad\quad\quad\quad \cdot \quad\quad \cdot & \\
\cdot \quad\quad \cdot \quad\quad\quad\quad\quad\quad\quad\quad\quad\quad \cdot \quad\quad \cdot & \\
a_{101}x_1 + a_{102}x_2 + a_{103}x_3 + \ldots\ldots\ldots\ldots + a_{1010}x_{10} &= n_{10}
\end{aligned} \qquad (8)$$

The coefficient a_{11} to a_{1010} are taken from Table 2, and the frequency distribution of φ_f is found.

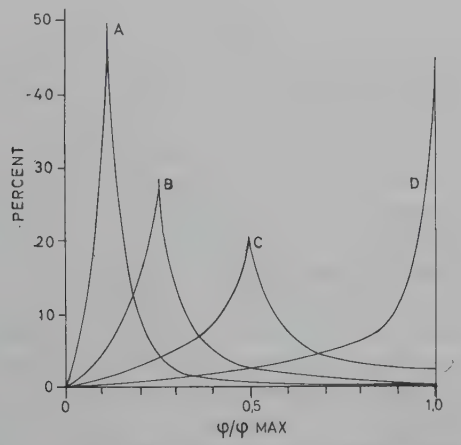

Fig. 4. Distribution in percent of φ/φ_{max} for φ_f/φ_{max} equal to *A*) 1/8, B) 1/4, *C*) 1/2 and *D*) 1.

Table 2. Frequency distribution in percent of φ φ_{max} for different ratios of φ_f φ_{max}. The fish is distributed and orientated at random with its long axis horizontally.

φ_f/φ_{max}	φ/φ_{max} 0	0.1	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9	1.0	Detectability in %
0	93	7	0	0	0	0	0	0	0	0		63
0.1	15	63	13	4	2	1	1	0	0	0		66
0.2	5	20	45	15	6	3	3	1	1	1		69
0.3	1	9	20	38	13	8	4	3	3	2		71
0.4	1	6	9	17	33	14	8	5	4	4		75
0.5	1	3	7	11	16	29	14	8	6	5		80
0.6	1	2	5	8	9	17	27	15	9	7		85
0.7	1	2	4	6	7	10	17	26	16	11		90
0.8	1	1	4	5	6	8	11	17	29	18		95
0.9	1	1	2	4	5	7	10	14	22	36		100
1.0												

RESULTS OF OBSERVATIONS

Observations of φ for cod and coalfish are shown in Fig. 5 A. Fig. 5 B presents corresponding distributions of φ_f as calculated from equation (8).

The target strength and length distributions from the same observations are presented in Fig. 6. The technique of observation is described by MIDTTUN (1966). The target strengt is calculated by a method similar to that described by CRAIG and FORBES (1969). However, only the maximum signal strength from each fish has been used, and it is assumed that this maximum occured when the fish passed the transverse axis of the beam. During all the observations the zero signal strength corresponded to a target strength of —40db.

In Fig. 7 the results of the analysis are shown in a φ_f — TS diagram. The two points are the mean values, and the rectangular areas are limited by the standard deviations of the observations.

Fig. 6 and 7 show that no significant difference was observed between the two species with regard to the target strength. This is not surprising as the lengths were approximately the same. The target strength values appeared to be rather low.

Regarding φ_f, however, a considerable difference between the two species was observed, and this might in future be used for identification purposes.

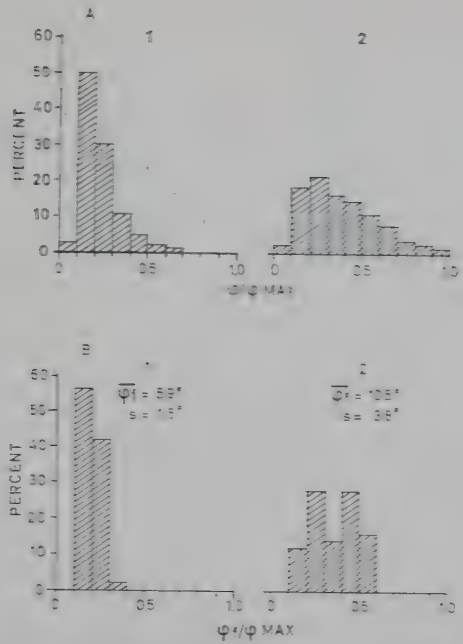

Fig. 5. Distribution in percent of A $\varphi \; \varphi_{max}$ and B $\varphi - \varphi_{max}$ for 1 coalfish and 2 cod.

DISCUSSION

The observed φ_t Fig. 5 were lower than those calculated from the measurements of Midttun and Hoff (1962). The mean lengths of the fish were, however, larger in the present experiments and therefore smaller fish angles may be expected.

Also the observed mean target strength were low as compared to the maximum values reported by Midttun and Hoff 1962 even though the fish were larger. This difference is probably caused by the fish under observation being more or less inclined from the horizontal. Most underwater pictures show that fishes are usually inclined relative to each other, and consequently they are also inclined relative to the horizontal plane. From this follows that field measurements of target strengths will always be low compared to the maximum values measured in laboratories.

If a mean inclination of 5° to the horizontal plane is introduced to the data of Midttun and Hoff (1962), the target strength of cod will

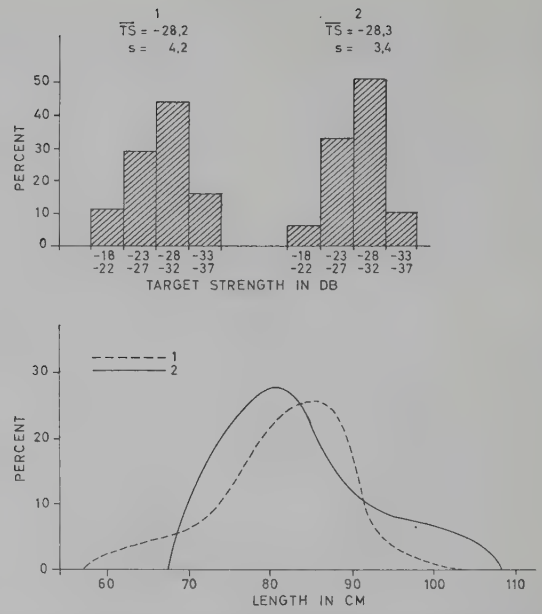

Fig. 6. Distribution in percent of target strength. 1) coalfish and 2) cod. Corresponding length distributions are shown below.

be reduced with a mean value of 5.5 db or, if the maximum dorsal aspect target strength of an 85 cm cod is taken to be — 20db, then the average inclination of the cod in our field observations is between 7 and 10°.

The detection sector angle, and consequently the fish angle as defined by us, will be influenced by the settings of the sounder. The difference obtained between cod and coalfish however, is not influenced by this since all the observations were made with the same sounder at the same settings. Another factor which will alter the detection angle, is the roll and pitch of the vessel (Fig. 4 Suomala 1970). As no measurements of pitch and roll angles were carried out, we were not able to analyse its influence on the results.

We assume the fish to be orientated at random but with the long axis in the horizontal plane. The first assumption was probably partly fulfilled by the pattern of different courses used during the observations. The second was, as already mentioned, not fulfilled. Considering the target strength measurements it is, however, not probable that the difference in fish angles between cod and coalfish should be caused by a

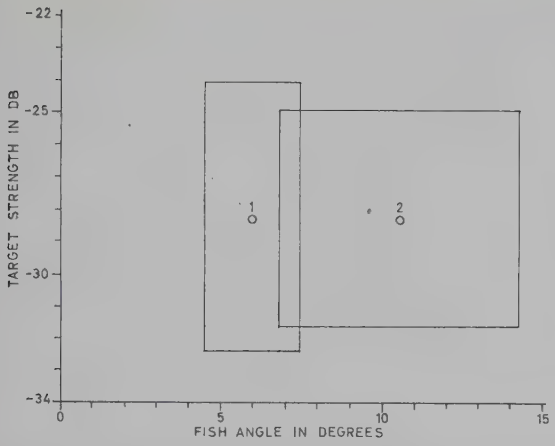

Fig. 7. Fish angle — target strength diagram showing mean values (circles) and standard deviations of observations (straight lines). 1) coalfish and 2) cod.

systematic difference in inclination between the two species during the observations.

The reason for this difference in fish angles is more likely to be found in the size and form of the swimbladders as pointed out by Midttun and Hoff (1962).

More experimental work should be carried out on a number of species and for different fish sizes in order to find out more conclusively whether the fish angle can be of general value as a tool in distinguishing between fish species as it would appears from our results on cod and coalfish. In future observations should be carried out with stabilized transducers in order to eliminate errors caused by the rolling of the ship.

ABUNDANCE ESTIMATION

METHOD

Methods of abundance estimation are described in Parrish (1969) and Anon. (1969). In the following the application of an echo integrator for the purpose of measuring fish density is explained.

The integrator was introduced by Dragesund and Olsen (1965) and has recently been modified (Bodholt 1969). The signal voltage is now squared before integration, and the output of the integrator is therefore proportional to number of fish both when multiple and individual fish targets are recorded.

Following Midttun and Nakken (1968) we write

$$M = C_1 \cdot N \qquad (9)$$

where M is the reading of the integrator, N is the number of fish giving this reading, and C_1 is the mean contribution to M from one fish.

When at constant fish density, ϱ (number per unit volum water) applying a TVG (time varied gain) proportional to the fourth power of the depth, the number of recorded fish will increase proportional to the square of the depth, D. For an integration over a given depth interval equation (9) can be written

$$M_D{}^4 = C_2 \cdot \varrho \cdot D^2 \tag{10}$$

where M_D4 is the integrator reading when the TVG is set proportional to the fourth power of the depth (40 log D), and D is the mean depth of the observed depth interval.

From (10) we get

$$\frac{M_D{}^4}{D^2} = C_2 \cdot \varrho \tag{11}$$

The expression on the left side is proportional to the integrator reading when the TVG is proportional to the second power of the depth (20 log D). Consequently, when a TVG proportional to the second power of the depth is used, the integrator reading will be proportional to fish density

$$\varrho = C_3 \cdot M_D{}^2 \tag{12}$$

The constant C_3 is now independent of depth, but dependent of target strength and φ_f and the characteristics of the sounder. If target strength and φ_f of the recorded fish are known, C_3 can be found. The most convenient way to find C_3, however, is to count single fish traces, say 30, on the paper record, calculate ϱ, and divide it with the corresponding $M_D{}^2$. The obtained value of C_3 can be used in equation (12) as long as the fish species and size remain unchanged.

DISCUSSION

It is important to determine if equation (12) is also valid for schools of fish. In other words, will one fish contribute to the integrator reading with the same value when member of a school as it does when recorded as an individual?

The sampling volume will increase with increasing school density which means that C_3 should be larger for fish as school members compared to single fish. The increment in C_3, however, will be small, and we consider it negligible.

In order to determine C_3, the sampling volume must be known. This can be found from the distribution of maximum target strength

of the fish and from the directivity pattern of the transducer. Due to the directivity of fish this procedure will give too low estimates of fish density as seen from Table 2. A transducer at the surface cannot detect fish with large values of α and X within the estimated angle, φ_{max}. The detectability decreases with decreasing φ_f. Probably, the fish is also inclined relative to the horizontal, and then the detectability in Table 2 will be further reduced. Therefore, for wide beam transducers the sampling volume should be calculated from the observed values of φ instead of from the directivity diagram of the transducer.

Equation (12) is not valid for large fish densities. From echo records we know that below dense fish schools the strength of the bottom echo is considerably reduced due to attenuation of sound within the school. In such cases values of ϱ calculated from equation (12) will be too low. However, at the front of the reflected signal from a school the attenuation might be neglected, and during the raise time of the echo the squared voltage should be proportional to the number of reflectors within one half pulsevolume. This then makes it possible to find the fish density in the uppermost part of the school.

The response of fish to the ship noise might cause a lower fish density within the field sampled with an echosounder. Olsen (1969) showed that a typical response of herring to an acoustic stimulus was to turn away from the sound source and swim towards the area of less sound intensity. It is not known, however, whether the fish will react in this way to the noise of a ship.

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COMPARATIVE ANALYSIS OF YEAR-CLASS STRENGTH AMONG FISH STOCKS IN THE NORTH ATLANTIC

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ABSTRACT

Dragesund, O. 1971. Comparative analysis of year-class strength among fish stocks in the North Atlantic. *FiskDir. Skr. Ser. HavUnders.*, *16*: 49—64.

A comparative analysis of year-class strength among stocks of abundant fish species (herring, cod, haddock, saithe, redfish and capelin) in the North Atlantic is given with a view to discussing whether covariation in year-class strength exists among species living in the same region and among stocks of the same species in different regions.

It is suggested that fish stocks of the same species living in regions distinctly separated from each other are independent and apparently no covariation in year-class strength exists among them. Even in neighbouring regions no apparent covariation could be found. Not all the species living in the same region produce numerous broods in the same year. Indications were found that the total number of 0-group fishes produced varied from year to year. It is tentatively concluded that the variation in total 0-group abundance did not vary to the same extent as the variation of the abundance of each of the species.

INTRODUCTION

In the present paper a comparative analysis of year-class strength in self contained stocks of abundant fish species, herring, cod, haddock, saithe, redfish and capelin, in the North Atlantic will be given. A similar analysis was made by Templeman (1965) with the view to discussing whether covaration in year-class strength exists among stocks of cod, haddock and herring living in different regions. This investigation also includes an analysis of year-class strength among fish species living in the same region.

More than one self contained stock (Anon. 1960) of each species may exist in the same region. Even if the fish stocks are self contained, a mingling of individuals from separated stocks may take place both within and between regions, especially during the feeding migration. Taking into account the general system of water currents in the North Atlantic

(Fig. 1) and the subdivision of fish species into large groups or populations, self contained fish stocks from five regions will be considered:

A) fish stocks which have their spawning grounds along the Norwegian coast, with nursery and feeding areas in the Barents Sea and the Norwegian Sea;

B) stocks which have their spawning grounds in western and northwestern part of the North Sea with nursery and feeding areas in the North Sea;

C) stocks which are spawning at South and West Iceland with nursery and feeding areas around Iceland and the Irminger Sea;

D) stocks which have their spawning, nursery and feeding grounds off West Greenland;

E) stocks which are inhabiting the banks off Canada and northern USA.

Generally a fish stock has separated spawning, nursery and feeding areas. The young drift with the current from the spawning to the nursery area (denatant movement). From the nursery area the juveniles usually recruit to the adult stock on the feeding area. The spawning migration

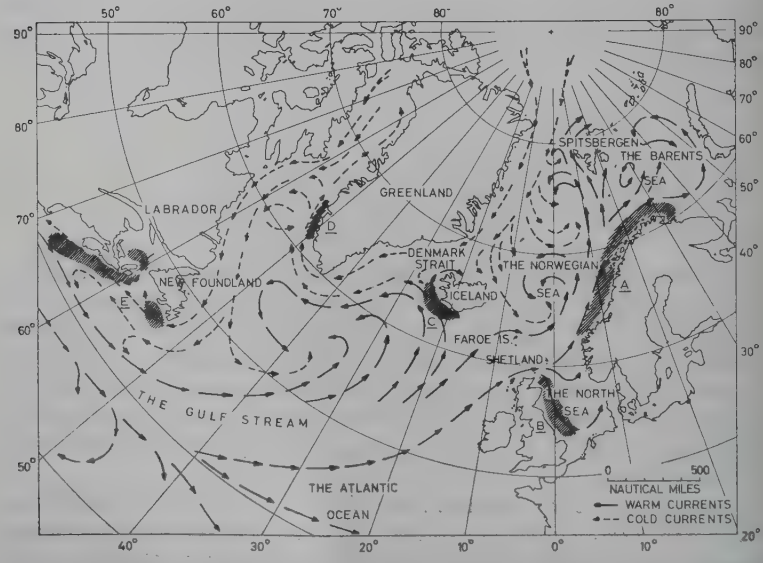

Fig. 1. The general surface water currents in the North Atlantic. Adapted from Mosby (1960). The diagonal shadings indicate some of the main spawning grounds in different regions.

from the feeding to the spawning grounds is against the current, (contranatant movement). Some of the stocks migrate via a wintering area on their way to the spawning grounds. The spent fish return to the feeding area with the current (Harden Jones 1968).

Special attention is paid to the drift migration phase of the young since this may be the most critical-period in a fish's life. Many species are drifting in the same watermasses simultaneously during the larval and postlarval stages, and during this period it is likely that there is a great competition for food. In order to understand the mechanism of year-class fluctuations of fish stocks within a region, research is needed on the interrelationship among species, e.g. time and location of spawning, drift pattern of the larvae and feeding behaviour of both the adults and the progeny. Knowledge about such interrelationships is necessary since a species cannot be studied in isolation, but must be investigated together with its biotic and abiotic environment.

The drift migration of the young is especially pronounced for fish in boreal regions. For most of the species the first part of this phase, when eggs and larvae are drifting passively with the current, lasts six to eight months for instance in region A). During this part of the life cycle the 0-group fish might be carried 500—800 nautical miles or even farther by the current (Dragesund 1970a, 1970b). The return migration from the nursery areas through the adult feeding area and farther on to the spawning grounds may take from three to eight years, for some species even longer, depending on their growth and maturing rate. To maintain their position within a region the older fish must undertake active and compensatory movements in the direction opposite to larval drift. This movement takes place usually in connection with the spawning migration, but both contranatant and denatant periodic migrations take place also during the adolescent stages.

In the present investigations two main questions are raised:

1) Does a covariation in year-class strength among stocks of the same species exist in neighbouring regions? Do the haddock stocks for instance in regions A), B) and C) produce abundant broods the same years?
2) Is the total number of recruits produced by all species in the same region varying from year to year?

MATERIAL AND METHODS

The major part of the material is obtained from:

1) records of age compositions from pre-recruit and adult stocks;
2) acoustic surveys of 0-group fishes.

YEAR-CLASS STRENGTH ESTIMATES BASED ON ANALYSIS OF PRE-RECRUITS AND ADULTS

Estimates of year-class strength for adults are complicated by the wide range of ages over which individuals of a given year-class attain sexual maturity. The most simple method used for estimating relative year-class strength is to compare the frequency distribution of the different year-classes in the exploited stocks. This method is used for Norwegian spring spawning herring combined with estimates on the adult stock size (Anon. 1970a, Dragesund 1970a). For cod and haddock the data are from ICES and ICNAF working group reports where the estimates are mainly based on pre-recruits (Anon. 1970a, 1970b, Graham 1969). For other species information has been placed at my disposal by colleagues at research institutes in England (Jones, personal communication), Scotland (Parrish, personal communication), Iceland (Jakobsson, personal communication) and USSR (Benko, personal communication). Due to the diffculties in obtaining comparable abundance indices year-class strength at age ≥ 3 years is indicated by grading it 1) very poor, 2) poor, 3) average, 4) strong and 5) very strong.

ACOUSTIC SURVEYS

0-group fish surveys in the Barents Sea have shown that many fish species occur pelagically, i.e. in the upper 100 metres of water in late summer and early autumn, and that it is possible from acoustic surveys combined with fishing by pelagic trawl to estimate year-class strength at an age of five to six months (Dragesund, Midttun and Olsen 1970). The 0-group fish investigations were started in 1959 (Dragesund 1970b), but prior to 1963 only herring were studied. Because of the promising results obtained for herring, other species were later included. The major laboratories conducting fisheries research in the Barents Sea took a joint initiative to carry out surveys and to expand the work to include all the commercially most important species; herring, cod, haddock, saithe, redfish, capelin, polar cod and long rough dab.

In order to obtain a more precise quantitative estimate of the total abundance of 0-group fish, and to reduce the element of subjectivity in the evaluation and classification of the echo sounder paper-recordings, an electronic echo integrator was developed to work in conjunction with

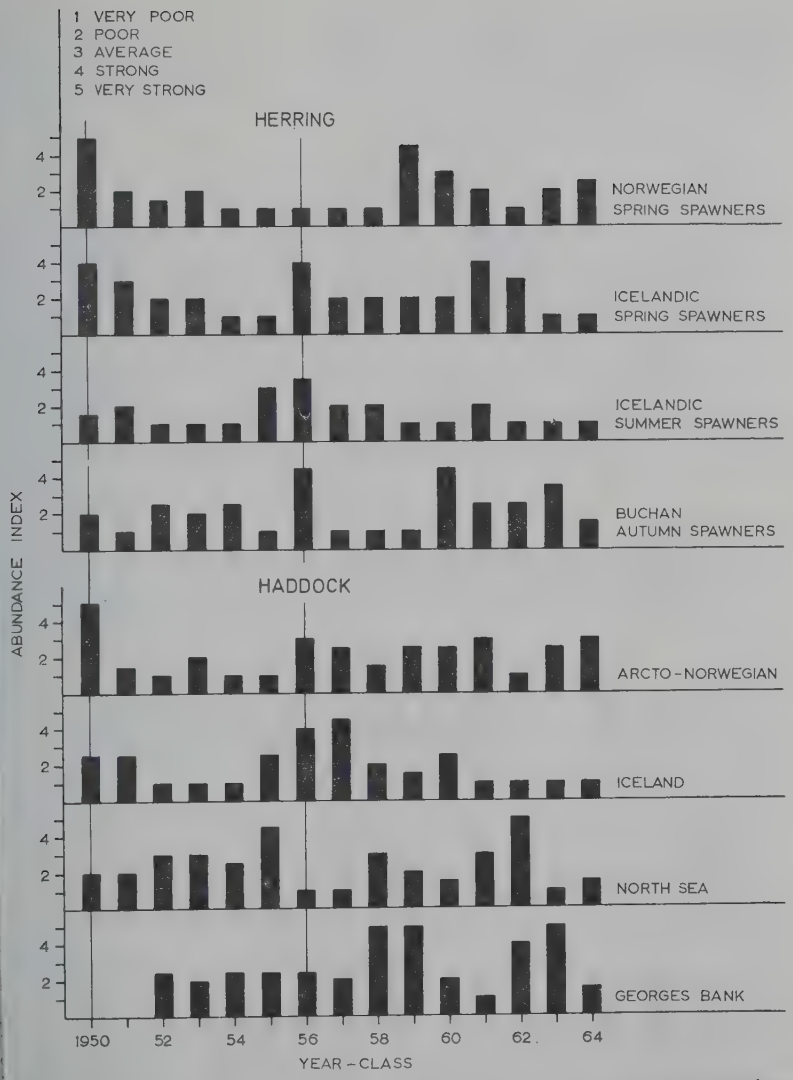

Fig. 2. Year-class strength at age $\geq$ 3 years of herring and haddock in different regions. The abundance estimates are indicated by grading year-class strength in, 1) very poor, 2) poor, 3) average, 4) strong and 5) very strong.

the acoustic research equipment onboard the Norwegian research vessels «G. O. Sars» and «Johan Hjort» (Dragesund and Olsen 1965). The echo integrator was first used during a cruise in the Barents Sea in

August—September 1963, and its technical performance proved to be successful. To facilitate comparison between years the sum of signal voltages per five nautical miles were plotted on charts, and isolines for equal levels of echo abundance were drawn.

RESULTS AND DISCUSSION

Fig. 2 shows year-class strength at age ≥ 3 years of herring and haddock in different regions. No apparent covariation in year-class strength among stocks of herring in the three neighbouring regions A), B) and C) could be found. The 1950 broods for example, were strong in Norwegian and Icelandic spring spawners, but not in Icelandic summer and in Buchan (North Sea) autumn spawners. The broods of 1956 were strong in all the herring stocks except in the Norwegian spring spawning herring.

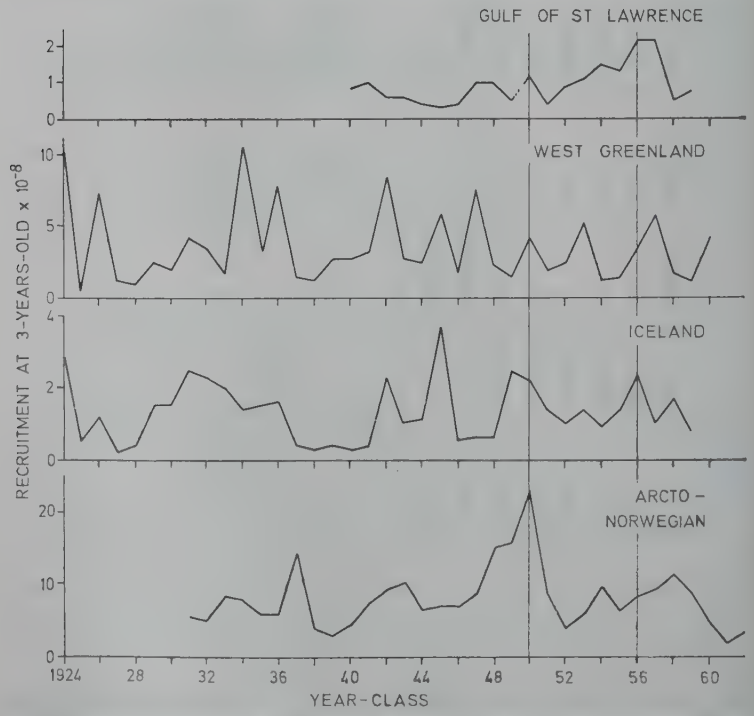

Fig. 3. Year-class strength at age ≥ 3 years of cod in different regions. Adapted from Garrod (1968).

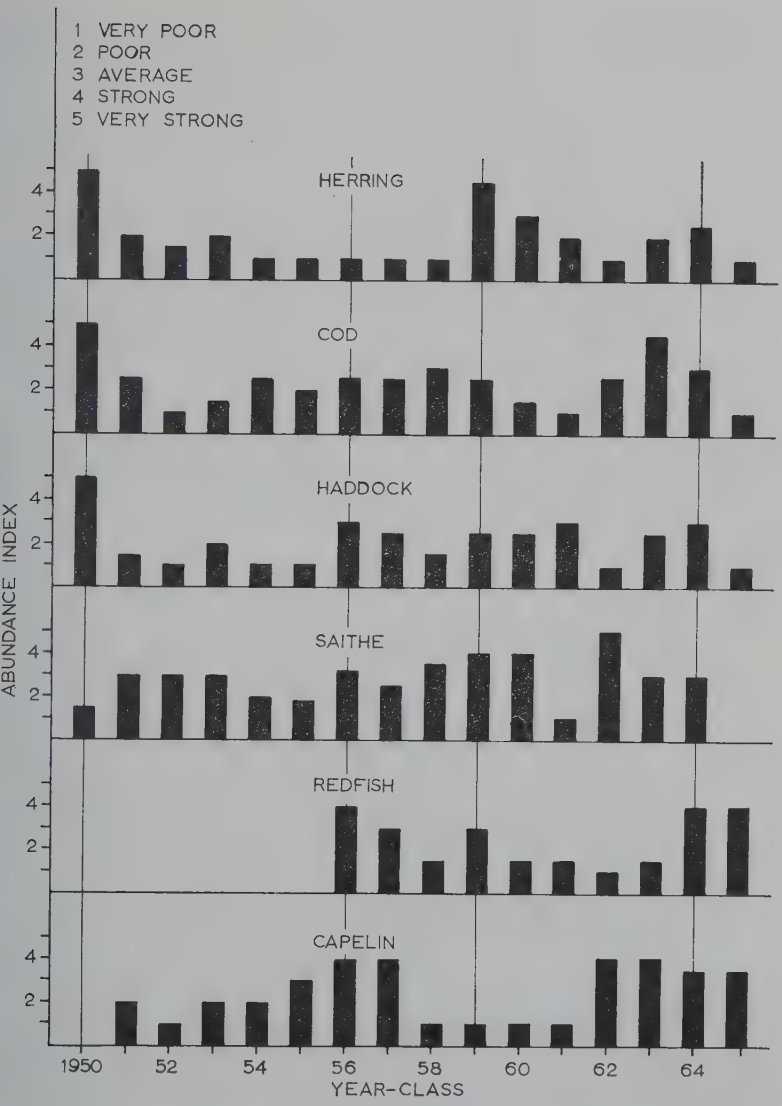

Fig. 4. Year-class strength at age ≥ 3 years for different species spawning at the Norwegian coast, region A). Year-class strength is grouped as, 1) very poor, 2) poor, 3) average, 4) strong and 5) very strong.

In the haddock stocks the 1950 broods were strong in the Arcto-Norwegian stock, but average or poor in the Icelandic and North Sea stocks. The broods of 1956 were average and strong in two stocks and very poor in one. Comparing also the year-class fluctuations of the Georges Bank haddock in region E) with haddock stocks living in regions A), B) and C) no covariation could be found.

Fig. 3 shows absolute recruitment in numbers of 3 year old fish in each year-class for different cod stocks in the North Atlantic (Garrod 1968). There was apparently no covariation in year-class strengths among the different stocks. The 1950 year-class was strong in the Arcto-Norwegian and in the Icelandic stocks whereas in the Northwest Atlantic stocks (Gulf of St. Lawrence and West Greenland) the year-class was about average in strength. The 1956 year-class was strong in the Gulf of St. Lawrence and Icelandic stocks, whereas in the other two stocks it was of average strength. In each of the stocks there seem to be periods of successful year-classes. In the Gulf of St. Lawrence stronger year-classes of cod were produced during the years 1955—1957 than in the period prior to these years. In the Arcto-Norwegian stock rich year-classes occurred in 1948—1950 whereas in the following years (1951—1956) relatively poor year-classes were produced. No apparent trend can be seen in the periodicity of these fluctuations.

In order to discuss the second question raised, year-class strength at age $\geq$ 3 years of six species; herring, cod, haddock, saithe, redfish and capelin spawning at the Norwegian coast i.e. in region A) is compared (Fig. 4). Unfortunately no data are available for redfish in the early 1950s. During the period 1950—1965 there was a clear tendency towards rich year-classes of several species, but not all the stocks produced abundant broods in the same years. However, in some years e.g. in 1950, 1956, 1959 and 1964 rich broods occurred in several stocks. This was the case for herring, cod and haddock in 1950, for capelin, redfish and partly saithe and haddock in 1956. In 1959 again a rich year-class of herring was produced, and the same was the case for saithe. In 1964 most of the broods were rich or average in strength.

To extend the series of observations and to compare year-class strength at an earlier stage, the abundance estimates from the 0-group fish surveys in the Barents Sea are considered. Fig. 5 summarizes the estimates of year-class strength at the 0-group stage of the different species investigated. Looking at the period 1963—1969 it will be seen that year-class strength of herring has been very poor except for the 1963 and 1964 year-classes which were of poor and average strength respectively. The year-class strengths of cod and haddock have varied, being very strong for cod in 1963 and average or strong in 1964 and 1969. Poor

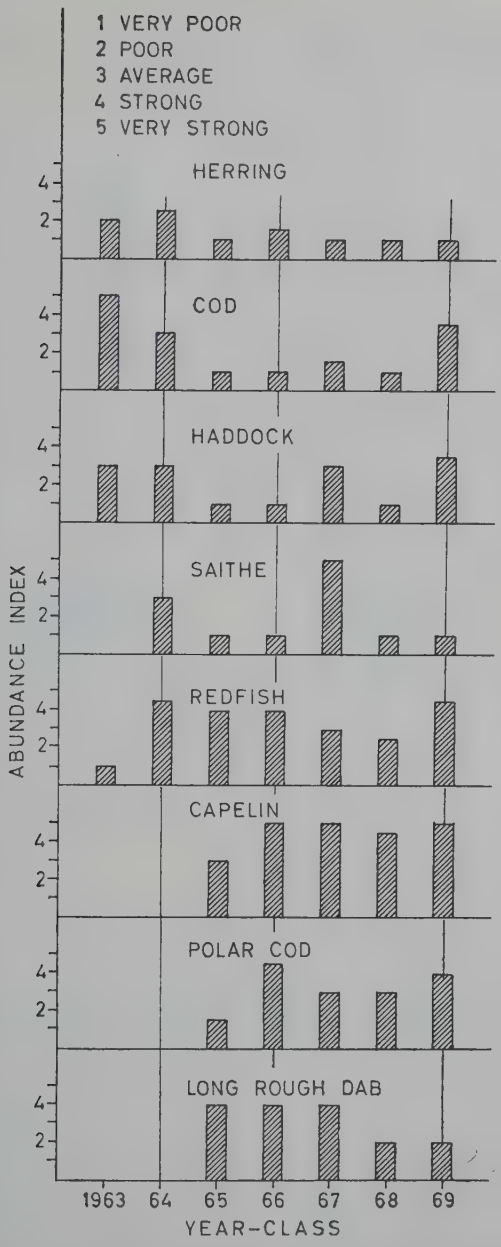

Fig. 5. Year-class strength measured at the 0-group stage for different species in region A). Year-class strength is grouped as, 1) very poor, 2) poor, 3) average, 4) strong and 5) very strong.

year-classes of cod were produced in 1965—1968. A similar trend in variation was found for haddock. The saithe followed the same variations as haddock except for the 1969 year-class. Redfish and capelin have been the dominating species during the years 1964—1969 with average or strong year-classes. It should also be noted that the stocks of polar cod and long rough dab have produced strong year-classes in some of the years during this period.

In order to compare year-class strength at the 0-group stage with subsequent year-class strength, the echo abundance of 0-group herring, cod, haddock and capelin is plotted against year-class strength at age ≥ 3 years grouped as very poor, poor, average, strong and very strong (Fig. 6). The 0-group echo abundance indices for herring are from Dragesund and Nakken (1970), for cod and haddock from Hylen and Dragesund (1970), and for capelin they are derived from Benko *et al.* (1970). A very close correlation is found between the two independent estimates of year-class strength, and it is concluded therefore, that the abundance indices of 0-group fish obtained from the acoustic surveys give a fairly good estimate of year-class strength.

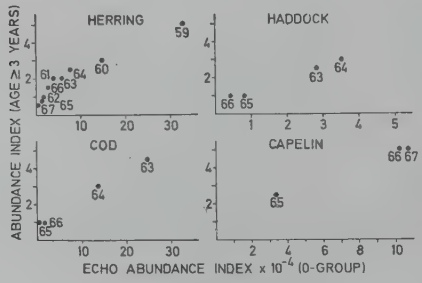

Fig. 6. Relationship between year-class strength at the 0-group stage and subsequent stages (age ≥ 3 years) for herring, haddock, cod and capelin in region A.)

The echo integrator readings showing the total echo abundance of 0-group fishes are given in Fig. 7. In 1963 only the central part of the Barents Sea was covered. Because of the differences in target strengths of the various species and echoes from other organisms than fishes, such as medusae, some caution must be used in interpretation, but it is sug-

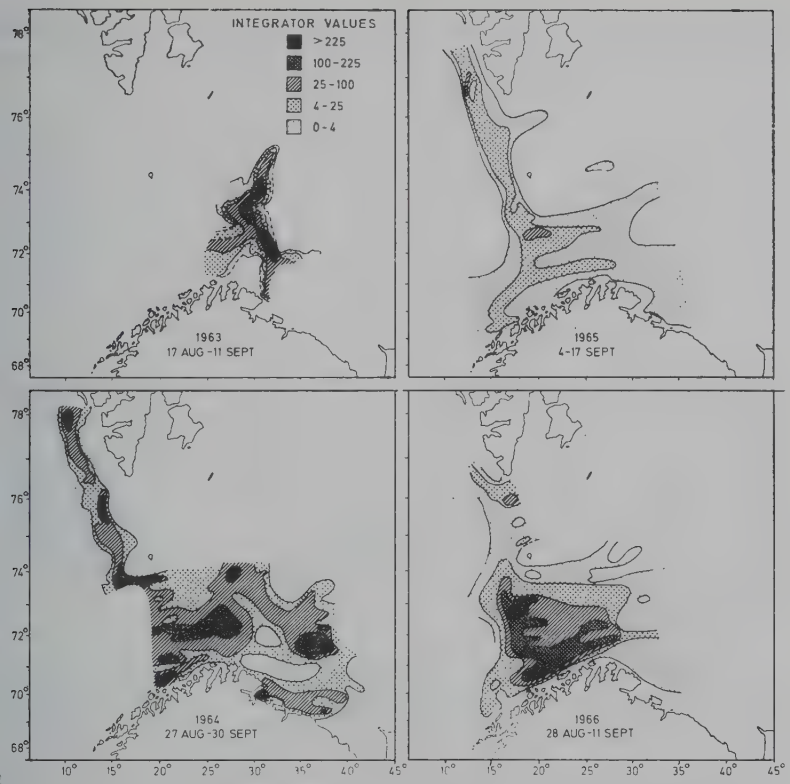

Fig. 7. Echo abundance distribution as determined by the echo integrator during the surveys in 1963 –1966. Equal levels of abundance are indicated by isolines.

gested that the total echo abundance varied from year to year. This is particularly pronounced when comparing the years 1964 and 1966 with 1965. However, the number of fishes might have been underestimated in 1965 compared with 1964 as long rough dab were numerous that year. This species as well as capelin have a lower target strength than the gadoids and herring which both had very low abundances in 1965.

No firm conclusion can be drawn concerning the variation in number of 0-group fishes from year to year, and more research has to be done in this field. However, it is tentatively concluded that the variation in the total number of 0-group fishes did not vary to the same extent as the variation in number of each of the species. One possible explanation

might be that there are interrelationships among species so that when the mortality of the progeny of fishes spawning earlier is high, then the progeny of species spawning next has a better chance of survival.

To illustrate the interrelationship among species the main spawning centres of saithe, haddock, cod, herring, redfish and capelin are mapped out (Fig. 8). The surface water currents are also shown in the figure. Plotting the spawning area against time of spawning (Fig. 9) it will be seen that spawning in region A) usually takes place comparatively later in the year for stocks spawning at the northern part of the coast. Due to the denatant movements of eggs and larvae and the difference in spawning time, all species will gradually mingle during the larval and postlarval phases.

To demonstrate a characteristic distribution of saithe, haddock, cod, herring, redfish and capelin at the 0-group stage 1967 has been chosen (Fig. 10). The 0-group herring had a restricted distribution with very low abundance. Similarly cod was recorded in a relatively small area, and no dense echo recordings were obtained. The abundance of 0-group haddock and redfish was estimated to be average in strength, whereas saithe and capelin were very abundant over relatively large areas.

The variation in total 0-group abundance is in one way or another related to the biotic and abiotic environmental conditions during the drift migration phase. The interrelationship among species is probably of great importance for the mechanism governing recruitment e.g. the

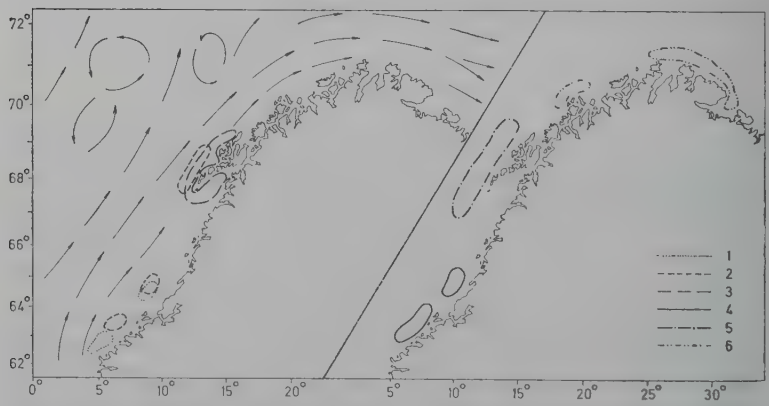

Fig. 8. Main spawning centres for, 1) saithe, 2) haddock, 3) cod, 4) herring, 5) redfish and 6) capelin in region A). The surface water currents are also shown in the figure.

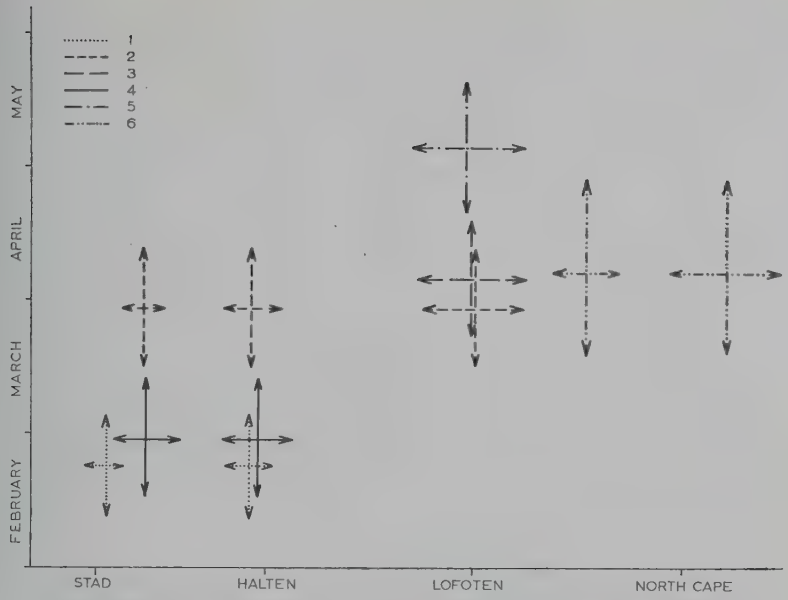

Fig. 9. Time of spawning in relation to spawning area. Legend as in Fig. 8.

predator effect. Gadoid fishes like saithe and haddock feed heavily on herring eggs (Dragesund and Nakken 1970), and later in the larval and post-larval phases both 0-group cod and haddock feed on 0-group herring and redfish (Wiborg 1960). Since there is a close correlation between 0-group abundance and subsequent year-class strength, it is likely that the relative proportion among year-class strength of the different species is established at a very young age, most likely during the larval and postlarval stage. It is unlikely that this proportion will be significantly changed later in life even though the carrying capacity in a region might be higher for some of the adult stocks. Recent investigations have shown that the stock size of herring has been of a much higher level than at present (Dragesund and Nakken 1970). It is likely therefore, that region A) has a far greater capacity at least for keeping the adult stock of herring at a higher level than at present.

The fact that not all the species produce numerous broods in the same year suggests that favourable conditions do not exist in a region for all the species to produce numerous year-classes. Lie (1966) has shown that the spawning time of *Calanus* varies from one year to another along the coast of Norway. The coincidence in time therefore between the occurrence of suitable food and hatching of fish larvae may be an important

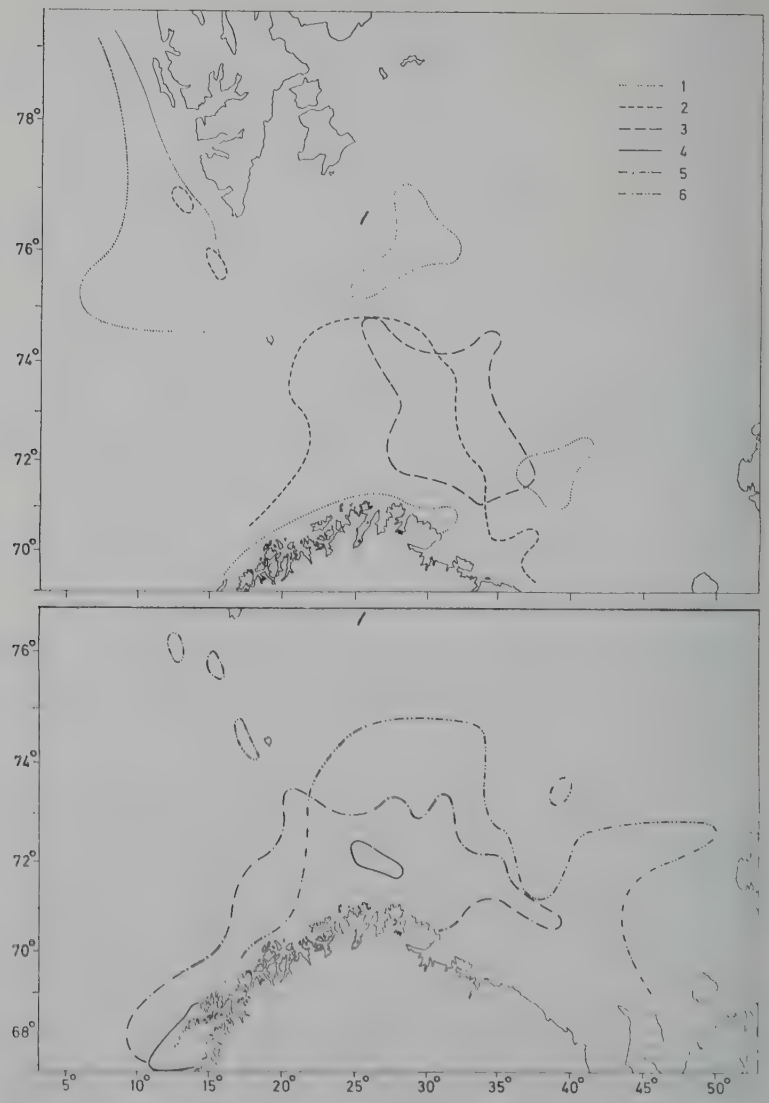

Fig. 10. Distribution of 0-group fishes in region A) during August—September 1967. Legend as in Fig. 8.

factor controlling year-class strength. The relationship between the spawning stock size the spawning potential and the resulting year-class is therefore often completely masked due to the great fluctuations in year-class strength that usually occur in boreal and subarctic regions. One is still left in doubt about the relative importance of the stock size and other conditions in determining year-class strength of fish stocks.

Knowledge of the pre-recruitment stocks therefore is essential in attempts to predict and control fisheries, and the advantage of knowing year-class strength for all species in a region before they are subject to fishing is obvious. This becomes even more important if the question of regulating the different stocks arises, and if a system of catch quota has to be introduced. So far the regulation has been concentrated too much on single species, and species of less commercial importance have been neglected. It is necessary to consider all species and estimate the total number of recruits produced in a region and try to find out its total capacity for producing recruits.

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FLUCTUATIONS IN YEAR-CLASS STRENGTH OF COD AND POLLACK IN SOUTHEASTERN NORWEGIAN COASTAL WATERS DURING 1920-1969

By

Stein Tveite

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ABSTRACT

Tveite, S. 1971. Fluctuations in year-class strength of cod and pollack in southeastern Norwegian coastal waters during 1920—1969. *FiskDir. Skr. Ser. HavUnders.*, *16*: 65—76.

From 1920 a small beach seine has every September—October (except 1940—1944) been worked at selected localities along the Norwegian Skagerack coast. The catch per beach seine haul of 0-group cod agree fairly well with catch per trap per week of the same year-class as I-, II-, III- and IV-group and may thus be used as estimate of the strength of each year-class. There are two marked periods with rich year-classes, one before 1930 and one after 1950. In the intermediate period the only rich year-classes were 1938 and 1945. The fluctuations are generally similar in all districts. There has been increase in relative abundance in the most open areas compared to the more landlocked ones. By the present method no effect of the liberation of cod larvae has been revealed.

The catch per beach seine haul of 0-group pollack is less reliable as estimates of year-class strength. Two rich periods, however, one before 1931 and one after 1953, are shown by the material. In the last period the average relative number is below that of the first period. Again, 1938 and 1945 are the only years in the intermediate period which gave rich broods.

Covariation between year-class strength of pollack and cod excist to some extent, but not all years with rich year-classes of one of the species showed a similar year-class strength of the other species.

INTRODUCTION

Along the Norwegian Skagerack coast small gadoids and other fish species have been sampled at a number of selected localities by a small meshed beach seine each autumn since 1917. Parts of the extensive material collected have been dealt with before (Løversen 1946 b, Dannevig 1949, 1954, 1959, Dannevig 1963). In some years during the period great quantities of cod larvae from Flødevigen hatchery have been liberated in the same area. Løversen (1946 b), Dannevig (1959) and Dannevig (1963) discussed the fluctuations in year-class strength measured as number of 0-group and 1-group cod caught by beach seine in relation to the

cod larvae liberated and the possibility of augmenting heavily exploited stocks of cod by artificial propagation.

The present paper describes variations in year-class strength measured by using the catch in a beach seine of 0-group cod, *Gadus morhua* L. and pollack, *Pollachius pollachius* (L). This method of estimating year-class strength is discussed later in relation to year-class strength measured as catch per trap per day. Possible covariations in year-class strength of the two species as well as factors (including artificial propagation) of importance for the strength of the year-class are looked for.

MATERIAL AND METHODS

The field work was performed during September—October. The total area covered is divided into 18 districts as shown in Fig. 1. Within each district were selected localities for operating the beach seine. Each district contain from two to nine such localities, and only localities examined throughout the entire period are considered here.

In districts 1—12 the sampling program was carried out during the whole period from 1917 to 1969; in district 13 (the Langesund district) from 1953 to 1969; in districts 14—18 (the Oslo fjord) from 1936 to 1969. There were no investigations from 1940 to 1944. In the years 1917—1919 the sampling was not carried out on all the localities used in later years and the results from these years are therefore omitted.

Up to 1961 a seine made of cotton was used. It was 38.0 m long and 3.8 m deep, and the mesh size was 14 mm stretched mesh. From 1962 a nylon seine of the same size and construction was used. No comparative experiments with the two seines were performed, but as no special change in number per seine haul and no special difference in length distribution of the fish caught in the two seines was found after 1961, the seines were considered to have the same fishing power.

The hauls were exactly taken at the same localities and covered the same areas each year. The seine was never operated by an entirely new crew in two successive years.

In each haul the numbers of different fish species were counted, and lengths were measured for cod, pollack, whiting, *Merlangus merlangus* (L) and coalfish, *Pollachius virens* (L). When the age-groups of cod were difficult to separate by length distributions, otoliths were used for age determination. Pollack was usually well separated in age-groups by length.

In Topdalsfjord and Søndeledfjord (Fig. 1) fishermen collected the biological samples from commercial catches taken by traps during the years 1922—1942. Near Biological Station Flødevigen (Fig. 1) fishing by two traps at fixed position started in 1924.

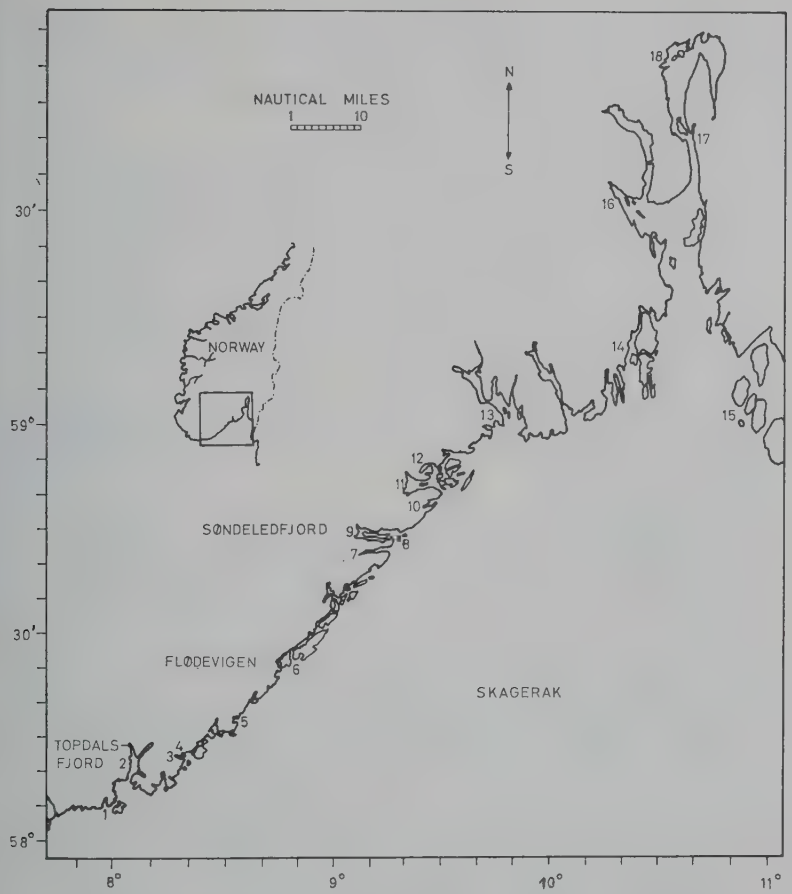

Fig. 1. Districts investigated. 1) Torvefjord, 2) Topdalsfjord, 3) Steindalsfjord, 4) Vestre Vallesvær, 5) Bufjord, 6) Flødevigen, 7) Sandnesfjord, 8) Søndeledfjord, 9) Risør Skerries, 10) Stølefjord, 11) Kilsfjord, 12) Soppekilen, 13) Langesund, 14) Vrengen—Tjøme, 15) Hvaler, 16) Holmestrand, 17) Drøbak, 18) Nærsnes—Bygdøy.

The age of the trap caught cod was usually determined from otoliths, occasionally from scales. The age of the pollack was determined from scales. A few fish were grouped into year-classes by length only.

RESULTS

COD

The catches of 0-group cod per seine haul are shown in Fig. 2, and an average for each district is indicated.

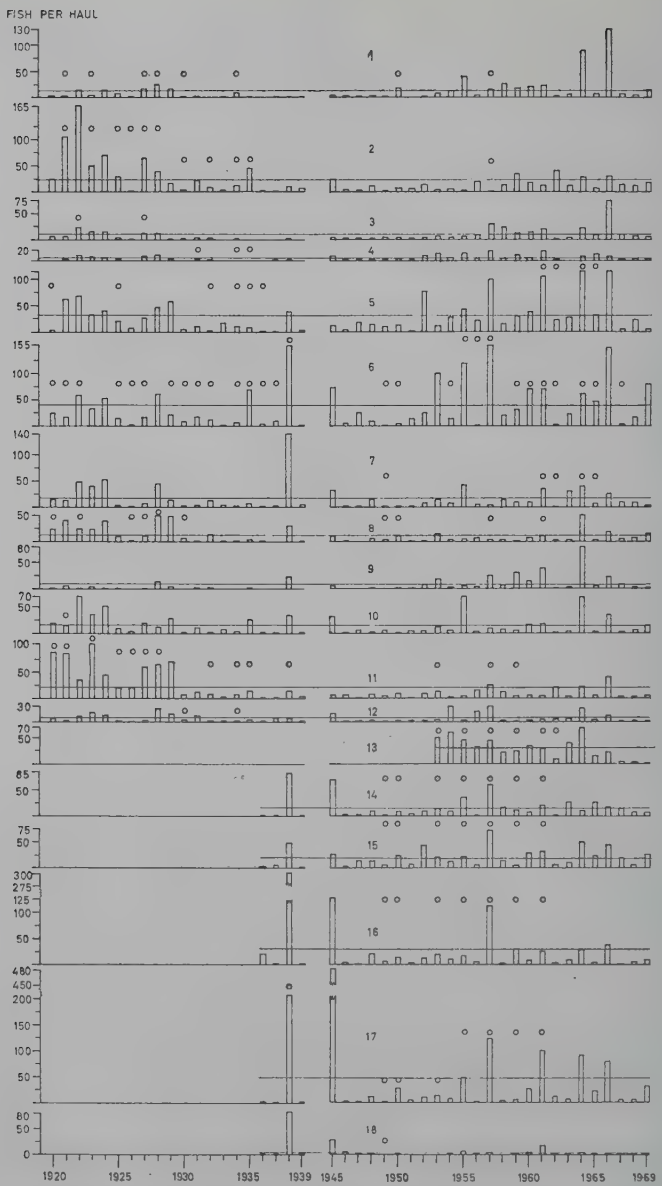

Fig. 2. 0-group cod per seine haul in the different districts. Average catch for each district is indicated. Liberation of cod larvae is marked by an open circle above the column. Districts numbered as in Fig. 1.

Table 1. Average number of 0-group cod per seine haul in five periods.

District	Periods				
	1920—29	1930—39	1945—54	1955—64	1965—69
1 Torvefjord	10.5	1.9	4.8	23.6	32.6
2 Topdalsfjord	56.8	11.8	8.2	17.9	16.3
3 Steinsdalsfjord	9.5	1.0	3.1	13.6	19.7
4 Vestre Vallesvær	5.9	0.4	4.4	8.2	4.8
5 Bufjord	36.1	9.3	18.0	50.8	34.9
6 Flødevigen	30.5	28.4	27.0	55.2	58.5
7 Sandnesfjord	24.3	18.3	8.4	19.6	9.6
8 Søndeledfjord	27.3	5.6	4.6	9.1	9.6
9 Risør Skerries	3.1	2.9	3.8	20.6	8.0
10 Stølefjord	25.8	8.4	6.8	20.0	12.1
11 Kilsfjord	59.7	6.8	5.9	11.6	11.7
12 Soppekilen	9.8	4.9	6.9	10.6	4.4
13 Langesund area				35.6	10.0
14 Vrengen—Tjøme			12.4	18.9	14.5
15 Hvaler			16.9	24.2	20.7
16 Holmestrand			21.9	24.2	11.4
17 Drøbak			56.6	42.3	29.2
18 Nærsnes—Bygdøy			3.2	3.4	1.3

By analysis of variance, the number of cod per beach seine haul has been found to be significantly influenced by both year and district ($P < 0.001$), quite apart from random variations and sampling errors.

Table 1 shows the average number of 0-group cod per seine haul calculated for four periods of 10 and one of 5 years. High catches per haul occurred mostly in the first and fourth period, and only 1938, 1945 and 1966 gave high catches in the other periods (Fig. 2). The averages for the ten years periods tended to be lower in the periods 1930—39 and 1945—54 than in the periods 1920—29 and 1955—64 except in the district Risør Skerries where a slightly lower average was found in the first period than in the period 1945—54 and at Drøbak where the best period was 1945—54. In three landlocked fjords at the Skagerack coast, Topdalsfjord, Søndeledfjord and Kilsfjord, a marked higher average of cod per haul was found in the first 10 years period than in any later period while in the more open fjords, Torvefjord, Flødevigen and Risør Skerries, the two last periods were the best ones (Table 1).

Of 29 years with investigations in the entire area clear differences in year-class strength in the different parts of the coast were only found in 1938, 1958 and 1959. In 1938 large numbers of cod were found east of Bufjord (district 5) while comparatively few were found farther west. In the two other years the higher numbers were found west of Bufjord.

Table 2. Relative numbers of 0-group cod caught in districts with and without liberation of cod larvae. See text for further explanation.

Year	Districts with liberation		Districts without liberation	
	Number of districts	Relative number	Number of districts	Relative number
1920	4	115	7	69
1921	5	135	7	140
1922	3	240	9	226
1923	3	148	9	180
1925	4	64	8	50
1926	4	20	8	8
1927	6	135	6	87
1928	4	213	8	267
1930	5	37	7	12
1931	2	66	10	56
1932	4	26	8	45
1934	7	35	5	9
1935	5	87	7	45
1938	4	274	13	372
1949	8	12	9	22
1950	8	75	9	35
1953	6	97	12	113
1955	6	149	12	158
1957	10	228	8	222
1959	7	56	11	115
1961	9	168	9	197
1962	4	28	14	63
1964	3	250	15	328
1965	3	85	15	72

Cod larvae were liberated in the districts where sampling by beach seine was carried out in years indicated by an open circle above the columns in Fig. 2. The figure shows no marked correlation between the catches of 0-group cod per haul and the liberation of cod larvae. In Table 2 the relative numbers of 0-group cod caught by beach seine in areas with and without liberation of larvae are compared. To have comparable figures, average number of 0-group cod per seine haul for the two periods 1920—1935 and 1936—1965 were calculated for each district, and for each district and year the numbers of 0-group cod caught per seine haul were converted to per cent of these averages. In some years considerably more 0-group cod were caught in districts with liberation of larvae (the same year) than in districts without liberation. However, in other years opposite results were obtained, and the average of the relative numbers for all years were nearly the same in both cases. In Table 3 the average number of cod per haul for years with liberation is com-

Table 3. Average number of cod per seine haul in years with and without liberation of cod larvae.

District	Number of years with liberation	Average number of cod per haul	Number of years without liberation	Average number of cod per haul
1. Torvefjord	8	11.3	37	12.9
2. Topdalsfjord	11	32.9	34	19.6
5. Bufjord	10	31.3	35	28.7
6. Flødevigen	28	36.3	17	40.2
7. Sandnesfjord	5	17.0	40	16.7
8. Søndeledfjord	10	14.2	35	10.6
11. Kilsfjord	14	38.1	31	11.8
13. Langesund	6	34.8	11	28.3
14. Vrengen—Tjøme	7	21.2	22	14.6
15. Hvaler	7	25.8	22	17.8
16. Holmestrand	7	32.2	22	28.0
17. Drøbak	8	67.3	21	38.7

pared with the average for years without liberation. Torvefjord and Flødevigen had, on the average, higher numbers of cod per haul for the years without liberation. In most of the districts, however, the two averages were more or less at the same level. As a source of variation in year-class strength, the liberation of cod larvae could not be significantly separated from other natural sources by the analysis of variance.

To compare the catches of the 0-group of a year-class in the beach seine and the later catches of the same year-class in the traps, the correlation coeffcients (r) between catch per seine haul and catch per trap per week of the same year-class as I-, II-, III-, and IV-group were calculated for the three areas where biological data was sampled from the trap catches. In Table 4 the coeffcients are given together with the significance levels (P) at which the values of r can be separated from zero. All coeffcients are statistical significant. In Topdalsfjord and Søndeledfjord there are fewer observation pairs, but both numerical value of r

Table 4. Correlation coefficients (r) between number of 0-group cod per beach seine haul and cod per trap per week of the same year-class as I-, II-, III- and IV-group and corresponding significance levels (P).

District	Year-classes	r	Value of P
2. Topdalsfjord	1923—1938	0.78	0.001
6. Flødevigen	1923—1963	0.37	0.02
8. Søndeledfjord	1921—1938	0.70	0.002

Table 5. Average number of 0-group pollack per seine haul in five periods.

Area	Periods				
	1920—29	1930—39	1945—54	1955—64	1965—69
1. Torvefjord	48.4	17.7	6.9	31.5	12.4
2. Topdalsfjord	7.6	6.0	4.2	5.2	1.5
3. Steindalsfjord	30.6	5.3	7.1	12.6	9.6
4. Vestre Vallesvær	16.0	5.5	5.2	8.1	4.1
5. Bufjord	45.1	14.5	9.1	8.5	5.2
6. Flødevigen	38.2	13.0	8.2	10.9	4.2
7. Sandnesfjord	25.0	11.3	8.9	6.1	3.1
8. Søndeledfjord	20.2	7.0	9.3	9.5	3.0
9. Risør Skerries	53.5	22.5	9.0	30.0	8.8
10. Stølefjord	41.2	14.9	8.2	18.6	8.9
11. Kilsfjord	17.8	4.5	5.9	7.5	1.0
12. Soppekilen	5.8	3.4	7.0	11.5	5.3
13. Langesund area				4.1	1.6
14. Vrengen—Tjøme			9.5	12.8	2.7
15. Hvaler			4.6	10.3	1.3
16. Holmestrand			2.1	4.8	0.2
17. Drøbak			5.1	16.2	1.0
18. Nærsnes—Bygdøy			1.5	4.4	0.1

and the significance level indicates a stronger correlation in these fjords than in Flødevigen.

POLLACK

The beach seine catches of pollack were also on average high before 1931, then low till 1953 except in 1938 in the Oslofjord district and in 1945 along the whole coast. After 1953 there have been more above average catches (Fig. 3). Variations between periods are not so evident as for cod, but the period 1920—29 had on average higher catches per haul than 1955—64 (Table 5). Only Soppekilen district has a higher average catch per haul in the period 1955—64 than in the period 1920—29.

By analysis of variance the number of 0-group pollack per seine haul is found to be significantly influenced by year and district.

No significant correlation between year-class strength estimated from beach seine catches of 0-group pollack and trap catches of older fish was found.

The catches of I-group pollack in the beach seine were incidental, probably because the pollack at this age schools in water deeper than normally fished by seine.

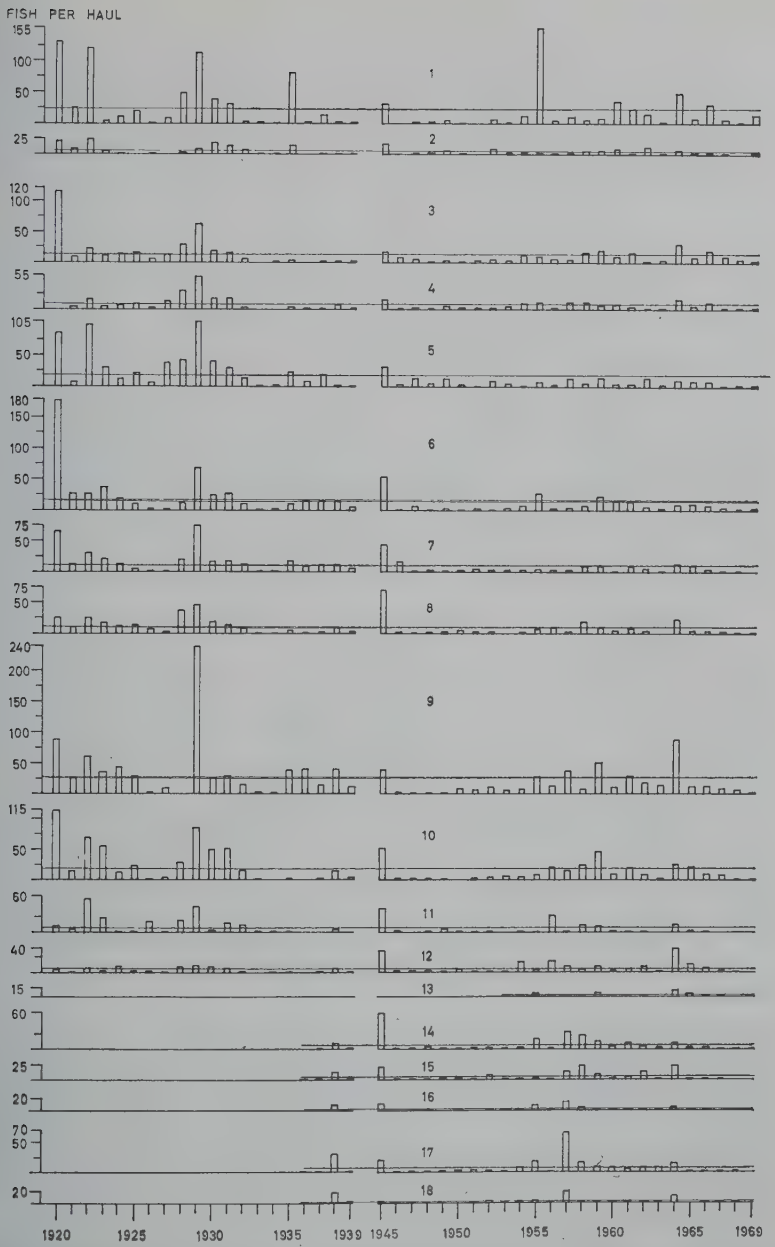

Fig. 3. 0-group pollack per seine haul in the different districts. Average catch for each district is indicated. Districts numbered as in Fig. 1.

DISCUSSION

Some of the one year old cod are caught in traps in deeper water, but some stay in the littoral region and are caught in the seine together with the 0-group. DANNEVIG (1963) found high correlation between quantities of I-group cod caught by beach seine and the quantities of 0-group cod caught the previous year.

Comparison between the 0-group catches and the trap catches of I- to IV-group cod the following years showed that the beach seine 0-group catches gave a relatively good estimate of the year-class strength (Table 4). The lower correlation coeffcient in Flødevigen is probably due to the trap sampling method used there, namely two traps at fixed depth and place all the year round. The efficiency of the traps may thus vary from year to year depending on temperature in the depths of the traps (DANNEVIG 1966). The fishermen in Topdalsfjord and Søndeledfjord used more traps (10—20 in Søndeledfjord and 5—10 in Topdalsfjord), and to get as big catches as possible, they placed the traps at the depths where the greatest concentrations of cod usually is found. These catches are therefore expected to be representative for the abundance of 1 to 4 year old cod.

Thus there is a good correlation between the catch of 0-group cod and the catch of I-group cod per seine haul (DANNEVIG 1963) and between 0-group cod per seine haul and I- to IV-group cod per trap per week. The year-class strength of cod may therefore be considered to be determined by the 0-group stage, and the catch per beach seine haul in the autumn is a good estimate of their relative strengths.

No statistical evidence was found for using the catch per beach seine haul of 0-group pollack compared with older age groups as an estimate of year-class strength. This is probably due to the method of sampling the older fish, the fishermen being more interested in the cod. However, the catch per beach seine haul of 0-group pollack varies significantly from year to year, and it is therefore suppodsed that the catches give indications of fluctuations in year-class strength.

Of the ten years with high catch per haul of 0-group pollack, seven years also gave a high catch per haul of cod. The conditions required to give rich year-classes may therefore be similar for cod and pollack, but small variations in the marine environment may influence the two species differently. For example the main spawning is somewhat later for the pollack than for the cod, and consequently the larvae of the two species may experience different food conditions.

If the year-class strength of cod measured by cod per beach seine haul is followed along the coast, it is found that the year-classes 1936, —39,

—46, —47, —48, —49 and —51 all showed year-class strength below average in all the fjords (Fig. 2). This shows that factors which cause poor survival of cod larvae at least have influenced some year-classes in all the districts investigaed. The strength of the rich year-classes varied more between districts than the strength of the poor ones, and therefore factors which cause favourable conditions for survival of cod larvae appears to be of a more local character.

Temperature influences the spawning time of cod (Dannevig 1959) and also the incubation time and growth of the larvae (Dannevig 1948, Shelbourne 1964). The stock size of many of the food organisms will probably also depend on the temperature. Thus the temperature during the spawning and hatching season is thought to be an important factor for determining the strength of the individual year-classes. Poulsen (1944) found a correlation between the year-class strength of cod in the Kattegat and the temperature in March—May. It has not been possible to find any correlation between the year-classes on the Norwegian Skagerack coast and the average temperatures measured every day at 0 m, 1 m and 15—20 m at Flødevigen. There may be a tendency for poor year-classes in years with great fluctuations in the temperature measured at a depth of 15—20 m, independent of the average value of the temperature.

It is known that the cod in the investigated area is relatively stationary (Løversen 1946 a, Danielssen 1969), and each fjord probably has its own stock (Dannevig 1966). Also the composition of ichtyoplankton is so different inside and outside the skerries that currents presumably bring about little exchange of spawning products (Dannevig 1922). The year-class strengths in each district are therefore dependent of the local spawning.

The observed decrease in year-class strength on sheltered localities in relation to more open localities might have been caused by a secondary pollution due to over-fertilization by sewage in sheltered localities and a positive effect of the fertilization in greater dilution in the more open areas.

Pollution might well have caused the reduction of cod in the inner Oslofjord (Ruud 1968). However, a similar effect can not be seen from the year-class strength of 0-group pollack in the Oslofjord. Dannevig (1959) suggested that this may be due to the late spawning when the polluting material, probably dangerous to the fish eggs and larvae, is more rapidly converted to harmless compounds.

The year-classes 1964 and 1966 showed that rich year-classes of cod still occur although not as rich in the most landlocked districts as in earlier years.

In years like 1950 there appeared to be more cod in the districts where larvae were liberated, but other years show the opposite result. In Table 2 half of the 24 years show better results in the districts where larvae were liberated. A comparison between years with liberation and years without liberation for the same districts shows a higher number of cod per haul in years with liberation for ten of the 12 districts (Table 3). However, by analysis of variance any effect of liberation of cod larvae can not be significantly separated from random variations. Thus it can be concluded that any positive effect of the artificial propagation has not been revealed by the beach seine method.

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THE RELATION BETWEEN THICKNESS OF CHORION AND SPECIFIC GRAVITY OF EGGS FROM NORWEGIAN AND BALTIC FLATFISH POPULATIONS

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ABSTRACT

Lönning, S. and Solemdal, P. 1972. The relation between thickness of chorion and specific gravity of eggs from Norwegian and Baltic flatfish populations. *FiskDir. Skr. Ser. HavUnders.*, *16*: 77—87.

Neutral buoyancy, size, and thickness and ultrastructure of the chorion were studied in eggs from populations of flatfish (*Platichthys flesus* and *Limanda limanda*) from western Norway and three localities in the Baltic: Kiel, the Arkona basin and Tvärminne. The observed differences in neutral buoyancy are probably caused by the differing thickness of the chorion and are correlated with the salinity in the area. The differences are thought to be the result of a long term selection process.

INTRODUCTION

Marine teleost species with pelagic eggs are often distributed over a wide range of salinities (Apstein 1910, Kändler 1941). Brackish water populations of such species produce eggs of a lower specific gravity, capable of floating in water of reduced salinity. Usually, but not invariably (see e.g. Mielck and Künne 1932), such eggs are bigger than those of marine populations of the same species.

Most authors have explained the low specific gravity of pelagic eggs in brackish waters as a function of the osmotic conditions, either in the ovary (Strodtman 1918, Solemdal 1967), or in the ambient medium (Jacobsen and Johansen 1908, Kändler and Tan 1965, Hohendorf 1968). The immediate osmotic effect on the specific gravity is, however, small, and can only explain part of the observed differences between the eggs of marine and brackish water populations. It has therefore been suggested that the existence of pelagic eggs with low specific gravity in brackish water populations is the result of long term selection (Solemdal 1971).

Interspecific differences in the thickness and ultrastructure of the chorion of pelagic teleost eggs have been described (Götting 1966, Hagström and Lönning 1968, Lönning 1972). As the chorion is the

Fig. 1. Sampling localities.

densest part of the egg, such changes have a marked influence on the specific gravity of the egg. To test the hypothesis that intraspecific variation in the chorion between marine and brackish water populations of a given species may be responsible for the observed differences in specific gravity, eggs from flounders [*Platichthys flesus* (Linnaeus)] and dabs [*Limanda limanda* (Linnaeus)] caught at Bergen and at different localities in the Baltic have been investigated with regard to size, neutral buoyancy, and thickness and ultrastructure of the chorion.

MATERIAL AND METHODS

Flounders (*Platichthys flesus*) and dabs (*Limanda limanda*) were caught near Bergen in water of 35 $^0/_{00}$ salinity and from Kiel Bay, 22 $^0/_{00}$ S. Flounders were also collected from the Arkona basin, 17—18 $^0/_{00}$ S, and from the area near Tvärminne Zoological Station, 6 $^0/_{00}$ S (Fig. 1).

Diameter and neutral buoyancy were determined on normally developing eggs 24 hours after fertilization, using the methods described by Solemdal (1967).

The fixation and embedding procedure for electron microscopy has been described by Lönning (1972). The material was sectioned on a LKB ultrotome III and examined in a Siemens Elmiskop I.

Ultrastructural studies were mainly carried out on eggs fixed 3—5 days after fertilization, and when nothing else is mentioned the micrographs are taken from this material. From the Bergen area unfertilized eggs and eggs fixed immediately after fertilization were also investigated.

RESULTS

Neutral buoyancy and egg diameter have been measured for eggs of populations of *Platichthys flesus* and *Limanda limanda*, living under different salinity conditions, and the results are given in Table 1. From this it can be seen that, in general, neutral buoyancy decreases with salinity, with the exception of the flounders from the most brackish area, Tvärminne, which have eggs of somewhat higher neutral buoyancy than those from the Arkona basin. In the Arkona basin the buoyancy is only just enough to keep the eggs from sinking, at Tvärminne flounder eggs sink and develop demersally. Similarly, egg diameter in both flounder and dab increases with decreasing salinity. Here again the sole exception are the flounders from the Tvärminne area, which have significantly smaller eggs than those from the Arkona basin.

Table 1. Neutral buoyancy and diameter of flatfish eggs from marine and brackish populations.

Species	Locality	Salinity ‰	Neutral buoyancy ‰ S	Pelagic: P Demersal: D	Egg diam. mm		Number of eggs	Individuals
					Mean	Range		
Platichthys flesus	Bergen	35	31.8	P	0.884	0.78—0.94	1 760	14
	Kiel	22	—	P	0.959	0.89—1.02	339	2
	Arkona	17—18	16.2	P	1.185	1.01—1.29	1 470	14
	Tvärminne	6	19.9	D	1.008	0.88—1.11	1 723	19
Limanda limanda	Bergen	35	30.9	P	0.770	0.75—0.87	332	7
	Kiel	22	17.5	P	0.928	0.84—1.04	485	7

In electron microscopic studies the chorion of the fish egg is usually described as consisting of a thin outer layer and a thick, lamellar inner layer. The nomenclature of these layers varies among authors; in this paper the purely descriptive terms «outer layer» and «inner layer» will be used.

Recent studies of the eggs of *Platichthys flesus* and *Limanda limanda* from the Bergen area have shown that the chorion of the egg has about the same thickness in these two species, viz. about 2.5 μ; the ultrastructure of the chorion, on the other hand, shows clear species-specific differences (Lönning 1972).

In eggs of *P. flesus* from Bergen the inner lamellar layer of the chorion consists of 6 lamellae and the distance between the lamellae varies, being largest between the mid-lamellae. Outside the lamellar part a reticular layer is present. The outer layer of the unfertilized egg is rather homogeneous whereas in the 3—5 days old larvae this layer is fenestrated or subdivided into several layers (Fig. 2, see also Lönning 1972, figs. 10, 12).

Eggs of *P. flesus* from Kiel Bay show a somewhat thinner chorion, viz. about 1.8 μ. Also in these eggs the number of lamellae is 6, but these lamellae seem to be more equidistant than in the Bergen material. The reticular layer and the outer layer are in these eggs more homogeneous and not so distinct (Fig. 3).

Eggs of *P. flesus* from the Arkona basin have a quite different chorion from those from the Bergen and Kiel area. The diameter is only ca. 1.1 μ and there are but three lamellae, of which the two outer are furthest apart. As in the Kiel material the outer and reticular layer are rather homogeneous, but in the Arkona population these layers are thinner (Fig. 4).

In eggs from Tvärminne, finally, the chorion is nearly as thick as in the Bergen material, viz. 2.3 μ. The number of lamellae, however, is only 4. Outside the lamellae a rather distinct, reticular layer is present, followed by the outer layer, which is often somewhat subdivided (Fig. 5). As mentioned above the eggs in this population are demersal.

The chorion of the egg of *Limanda limanda* from the Bergen area has been described earlier (Hagström and Lönning 1968, Lönning 1972). As already mentioned the diameter is 2.5 μ. In this species the lamellar part consists of 9 equidistant lamellae and the outer layer is subdivided into several homogeneous layers of different electron density (cf. Fig. 6, which shows an unfertilized egg).

Eggs of *L. limanda* from Kiel (Fig. 7) have a thinner chorion, viz. 1.6 μ. The number of lamellae is 8 or 9, and also in this population the lamellae are equidistant. The outer layer is less homogeneous than in

the Bergen material, and is somewhat broken up. As the Kiel material consisted of 5 days old larvae, some of these differences, especially in the outer layer, may be due to morphological changes during development (cf. Lönning 1972).

A synoptic comparison of the data on the ultrastructure of the chorion in the investigated populations of *P. flesus* and *L. limanda* is given in Table 2.

Table 2. Diameter of chorion and number of lamellae of flatfish eggs from marine and brackish populations.

Species	Locality	Chorion		Number of eggs measured
		Thickness μ Mean	Number of lamellae	
Platichthys flesus	Bergen	2.5	6	13
	Kiel	1.8	6	5
	Arkona	1.1	3	5
	Tvärminne	2.3	4	6
Limanda limanda	Bergen	2.4	9	11
	Kiel	1.6	8—9	6

DISCUSSION

The low specific gravity of pelagic fish eggs in brackish areas is of survival value as it will cause the eggs to float in water of lowered salinity.

Short term experiments with flounders which were transferred from high to low salinity showed that the specific gravity of the eggs was little affected (Solemdal 1967). Similarly, Baltic flatfish kept for two years in water of full marine salinity still produced eggs of low specific gravity (Solemdal, in press). The differences in neutral buoyancy in pelagic eggs of marine and brackish water populations of the same species can thus not be explained by water absorption by the eggs due to osmotic conditions in the ovary or the surrounding medium.

Of the different egg components, the chorion is by far the densest. In herring the chorion amounts to 15–30% of the total dry weight (Blaxter and Hempel 1963), in plaice 19–33% (Solemdal 1970).

Generally the Baltic populations have eggs with a thinner chorion than the marine populations (Table 2). In *Platichthys flesus*, fishes from the Arkona basin have the thinnest chorion, while at Tvärminne, in still

more brackish water, the chorion is much thicker and has in fact nearly the same value as in the marine populations. However, at Tvärminne the eggs develop at the bottom, so that a thick, tough chorion is a definite advantage.

Both the thin chorion of the most brackish populations, and the thick chorion of the Tvärminne flounders, may thus well be the result of a long term selection process. This hypothesis is supported by the experiments mentioned above, in which it was shown that in Baltic flatfish kept at high salinity for as much as two years the eggs still were of the low gravity Baltic type. Differences in e.g. feeding conditions, hydrography or spawning season in the Baltic populations can thus be ruled out as a possible explanation for the differences in egg structure.

In both *Platichthys flesus* and *Limanda limanda* there is an inverse correlation between diameter of the egg and its specific gravity (Table 1). Such a correlation does not exist, on the other hand, in *Pleuronectes platessa*. In this species the Baltic populations have the smaller eggs (Solemdal, in press). Egg size per se is thus not likely to be the main cause of the observed differences in specific gravity.

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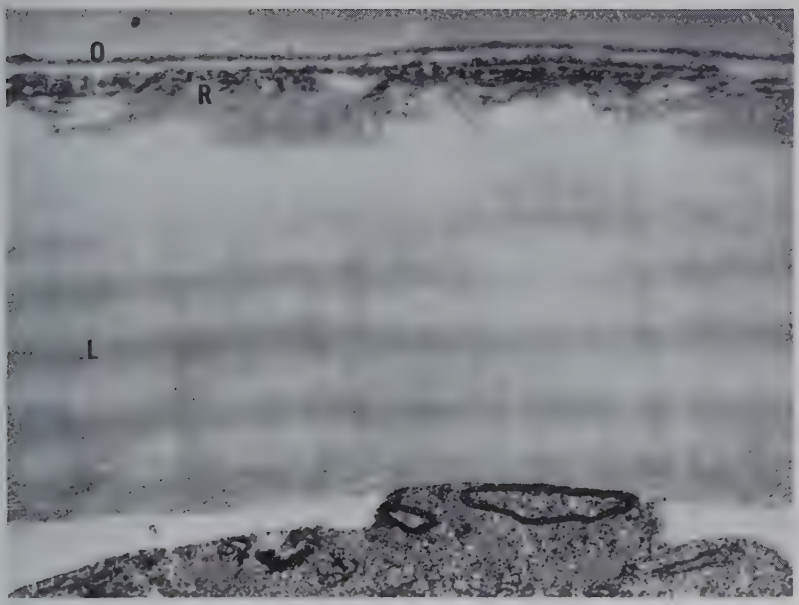

Fig. 2. Chorion with outer layer (O) and inner layer consisting of a reticular part (R) and 6 lamellae (L). 30 000x. *Platichthys flesus* from the Bergen area.

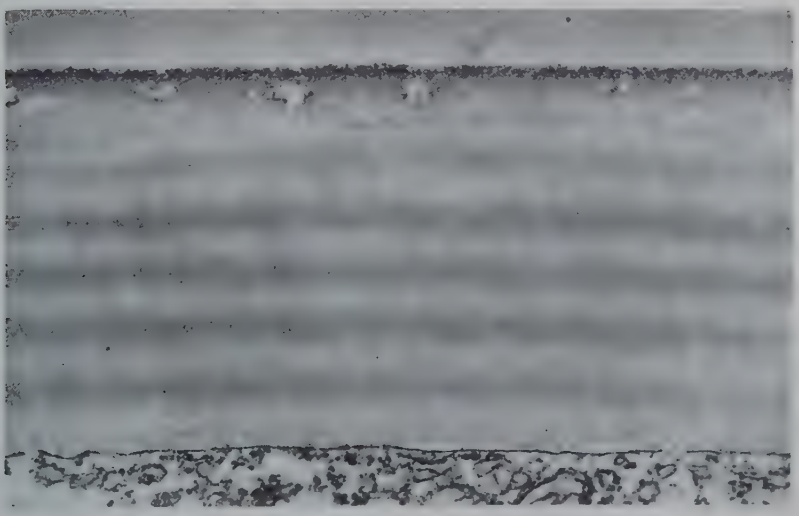

Fig. 3. *P. flesus* from Kiel Bay. 30 000x.

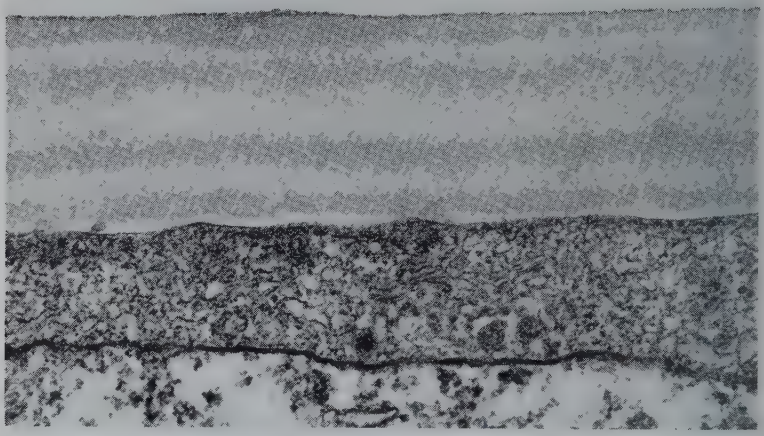

Fig. 4. *P. flesus* from the Arkona basin. 30 000x.

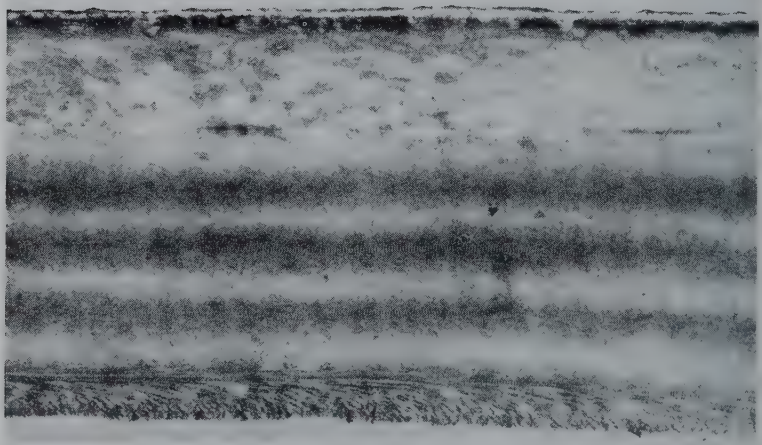

Fig. 5. *P. flesus* from the Tvärminne area. 30 000x.

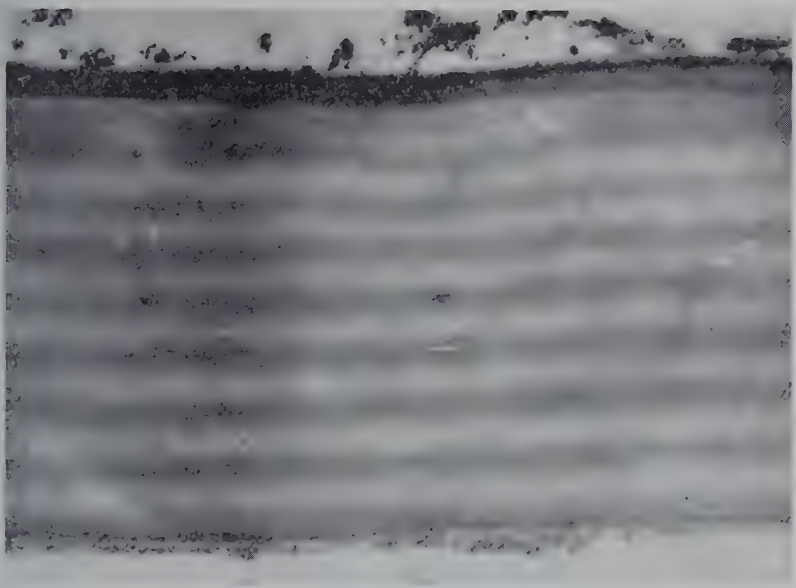

Fig. 6. *Limanda limanda* from the Bergen area. 30 000x.

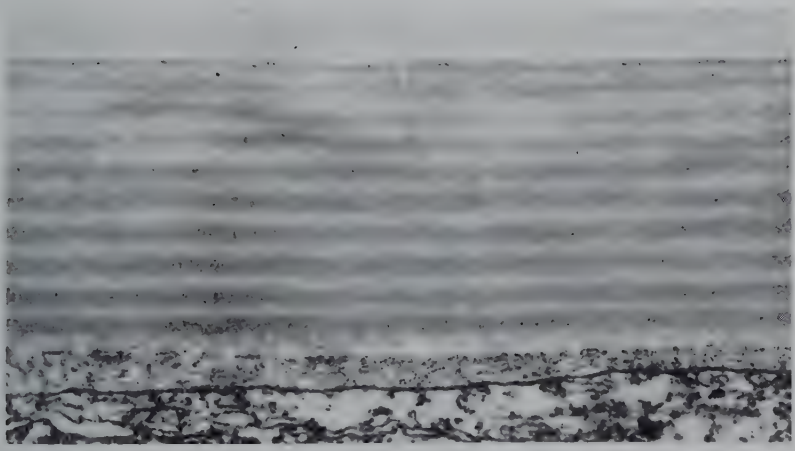

Fig. 7. *L. limanda* from Kiel Bay. 30 000x.

FiskDir. Skr. Ser. HavUnders., 16 : 89—97.

NOTES ON THE GAS CONTENT AND NEUTRAL BUOYANCY IN PHYSOSTOME FISH

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ABSTRACT

Sundnes, G. and Bratland, P. 1972. Notes on the gas content and neutral buoyancy in physostome fish. *FiskDir. Skr. Ser. HavUnders., 16* : 89—97.

Field and experimental observations from herring (*Clupea harengus*) and char *(Salmo alpinus)* indicate that the swimbladder gas is not only «swallowed» from the atmosphere, but may also be deposited from the vascular system or tissue around the swimbladder lumen.

INTRODUCTION

The genera Salmo and Clupea are both physostomes and do not possess any organ or rete formations similar to those of the physoclists (Fahlen 1967, 1971).

The ethology of the two species is fairly similar. They are schooling fish which live in deeper water during feeding periods but move to shallower areas to spawn. During migration to shallower areas the herring undergo a vertical migration resulting in reduced hydrostatic pressure. The herring avoid overflotation by releasing gas. Prior to the development of acoustical instruments, one of the methods of herring detection in the spawning areas was the observation of the numerous gas bubbles coming to the surface.

The char gas release is of a more complicated nature. The char do not only release gas to compensate for a decreasing hydrostatic pressure. They also release gas by emotional stimuli when the fish are in a steady state of hydrostatic condition (Sundnes, unpublished observations). A similar behaviour has been described in the European minnow (Dykgraaf 1932) and in some North American physostome fish (Verheijen 1962).

The gas filling mechanism for herring and char is not known in detail. However, Clupeids are able to swallow gas at the surface (Srivastava 1964, Fahlen 1967) and a similar function was described also for Salmonids (Jacobs 1934).

On the other hand, Wittenberg (1958) has described the refilling of emptied swimbladders of Salmonids in 13 days due to secretion. Fahlen (1971) was not able to confirm the findings of Wittenberg (1958), but in his experiment the fish had a gas content of 1.2 cc after 40 days.

The present work intends to give more information about swimbladder function of the fish in their natural environment.

MATERIAL

Local herring (*Clupea harengus*) from the Trondheims fjord and the Lindåspoll have been used. They are more or less available the entire year and were caught by hook and line or by gillnets. For comparative reasons char (*Salmo alpinus*) from Grimevatnet, Vangsvatnet near Bergen and Øvervatnet in Salangen have been studied. The char were caught by gillnets and beach seine. The reason for using char as a comparative fish in this study is not only the similar ethology with respect to hydrostatic pressure, but also the far better resistance of the char against experimental stress. Both herring and char were transported to the institute of Marine Research for experimental work.

METHODS AND RELIABILITY OF DATA

The swimbladder gas was analysed using the 1/2 cc analyzer (Scholander 1947) in the laboratory experiments. In the field work the «water analyzer» (Scholander, van Dam, Claff and Kanwisher 1955) was used. The accuracy of the latter is not good enough for CO_2 analysis, but accuracy of the values of the gas mixtures found in the physostomes (Sundnes 1963, Sundnes, Bratland and Strand 1969) are determined by the accuracy of the analyzer which is $\pm$ 0.3 per cent of the true value.

Buoyancy tests were performed by weighing the gas free fish under water as described by Saunders (1953). The volumetric measurement of the gas content gave the depth of buoyancy by using following equation: Depth of buoyancy $= \frac{\text{Gas volume}}{\text{Weight of the submerged fish}}$.

A measurement of the buoyancy of physostomes like herring and char by method mentioned above is not precise. By taking the fish from the depth of catch the swimbladder expands and thereby some gas is released.

Buoyancy measurements of char are more problematic as it releases gas even in a buoyant condition by emotional reactions. The buoyancy determinations will therefore always give minimum values. The swimbladder gas pressure relative to the surrounding hydrostatic pressure was measured by transducers (Sundnes and Gytre 1972, in press). These measurements were carried out in aquaria. These results are also influenced by the emotions of the fish. In experiments it is difficult to decide which aspect of the behaviour is imitated in the instinctive system of the fish. To make the fish cooperate in aquaria and obtain data which is relevant to the open sea is, therefore, difficult in many cases. The fish have been observed in field by various types of Simrad echo sounder.

RESULTS AND DISCUSSION

The value of the CO_2 and O_2 contents found in the swimbladders of herring in the Trondheims fjord at 8 m depth under a pressure condition where they released gas (millions of gas bubbles reaching the surface over the whole visible area) are given in Table 1.

Table 1. Gas content in *Clupea harengus* from Trondheimsfjord caught by hook and line.

Fish no.	CO_2%	O_2%
1	0.1	15.5
2	0.1	8.5
3	1.1	17.9
4	1.2	16.00
5	1.2	18.6
6	1.2	19.7
7	0.1	12.7
8	0.8	18.3
9	1.1	10.4

The oxygen content of the swimbladder varied from 8.5 to 18.3 vol%. In herring from the Lindåspoll the oxygen content varied over the same range as in the Trondheims fjord herring, i.e. 7.7 to 17.7 vol% (Table 2).

As far as the gas data are concerned, the oxygen values do not indicate that the swimbladder gas originated from the vascular system of the fish. A gas content of > 21 vol% oxygen would evidently indicate that the oxygen in the haemoglobin of the vascular system of the fish could play an important part as the source of the swimbladder gases. The field studies have not so far indicated the possibility that the oxygen originates from the haemoglobin of the vascular system.

Table 2. Gas content in *Clupea harengus* from Lindåspollen.

Fish no.	CO_2%	O_2%
1	0.6	14.8
2	0.5	16.1
3	2.3	17.5
4	1.2	16.7
5	0.8	17.33
6	0.6	16.1
7	0.1	9.33
8	0.2	16.9
9	0.3	10.4
10	0.8	7.7
11	0.4	10.6
12	0.9	13.3
13	0.4	17.7
14	0.5	17.6

Table 3. Gas content in *Salmo alpinus* from Randsfjorden.

Depth in meters	CO_2%	O_2%
70	0.22	2.91
»	0.33	13.26
»	0.15	3.60
»	0.17	15.87
»	0.29	2.96
»	0.30	15.23
»	0.18	2.88
»	0.29	10.06
»	0.23	3.80
»	0.27	14.30

The oxygen content found in the swimbladder of the char is also lower than the atmospheric value. In general, the oxygen values from char in normal conditions in nature are lower than those found in herring. In Table 3, 4 and 5 the O_2 content with the respective CO_2 values from different localities and depths are listed.

While the values for the gas mixture found in herring and the char do not exclude the possibility that the gas has been «swallowed» directly from the atmosphere, they are more consistent with the findings of Jacobs (1934), Srivastava (1964) and Fahlen (1967). On the other hand Wittenberg (1958) and Fahlen have described a refilling of the swim-

bladder in Salmonids independent of an air swallowing function. They found that the gas content of the swimbladder mainly consisted of nitrogen. The refilling process was very slow and incomplete in the fishes used by Fahlen (1967) compared to those used by Wittenberg (1958).

Table 4. Gas content in *Salmo alpinus* from Grimevatnet.

Depth in meters	CO_2%	O_2%	Depth in meters	CO_2%	O_2%
20	0.35	5.70	30	0.31	3.67
»	0.70	12.02	»	0.18	9.45
»	0.42	3.99	»	0.17	4.27
25	0.43	2.88	32	0.62	10.77
»	0.47	3.52	»	0.55	12.96
»	0.43	9.31	50	0.14	4.22
27	0.47	11.24	»	0.38	16.15
»	0.48	1.96	»	0.22	6.11
30	0.30	9.30	»	0.26	3.32
»	0.43	14.54	»	0.13	2.47
»	0.36	5.14	»	0.12	3.10
»	0.41	12.21	»	0.13	2.87
»	0.43	2.21	70	0.18	0.68
»	0.40	9.08	»	0.14	4.91
»	0.20	0.51	»	0.20	4.66
»	0.42	10.20	»	0.17	6.88
»	0.48	15.60			

In the latter experiments, the high nitrogen content does not indicate the source of the gas. It is doubtful that the primary gas deposited in the swimbladder consists mainly of nitrogen. As long as the composition of the residual gas in the swimbladder is unknown, any refilled gas will be «contaminated» by the residual gas (Sundnes *et al.* 1969). Also, the delay between the deposition of gas and the gas sampling is important (Sundnes *et al.* 1969). In the present work char have been emptied of swimbladder gas to the degree which is possible by puncture and then kept in aquaria with no access to the surface. The fish were then emptied of gas in intervals varying from 3 to 9 days. The results of the gas analysis for a char are shown in Table 6.

Table 6 shows a high degree of variation of the oxygen content in the refilled gas. The oxygen content of the primary refilled gas is not known as long as the residual gas volume is unknown.

The high nitrogen content found in the refilled gas by Wittenberg (1958) is possibly caused by the secondary effect described by Sundnes *et al.* (1969). The relatively high oxygen content found in the present

Table 5. Gas content in *Salmo alpinus* from Øvervatnet.

Depth in meters	CO_2%	O_2%	Depth in meters	CO_2%	O_2%
6	0.39	15.39	23	0.11	5.56
»	0.28	19.07	»	0.06	11.86
9	0.59	13.24	»	0.10	14.36
»	0.75	16.32	»	0.12	6.10
»	0.45	12.00	25	0.73	19.88
»	0.40	16.64	»	0.53	19.68
12	0.34	15.77	»	1.48	19.40
15	0.39	15.46	»	0.11	20.83
18	0.42	20.10	»	0.06	19.53
»	0.03	6.78	»	0.11	18.69
»	0.11	8.47	»	0.17	15.39
»	0.29	16.49	»	0.17	18.46
»	0.17	17.19	»	0.10	17.09
»	0.06	18.61	»	0.06	18.10
»	0.22	5.86	»	0.06	16.07
20	1.50	13.10	»	0.16	17.56
»	0.80	3.90	»	0.02	19.70
»	0.10	18.10	»	0.12	15.66
23	0.18	9.66	»	0.04	17.94
»	0.10	19.44	»	0.14	2.49
»	0.18	18.62	»	0.19	5.33
»	0.14	17.56	30	1.00	0.00
»	0.30	12.53	»	0.44	3.40
»	0.07	8.57	»	0.35	7.20
»	0.18	10.72	»	0.70	2.30
»	0.11	18.85	»	1.30	4.20
»	0.31	18.41			

Table 6. Gas content of char with no excess to surface.

Date		vol. of gas sample	CO_2%	O_2%
16/11	original gas	5	0.93	15.81
25/11	refilled gas	6	1.05	9.90
1/12	refilled gas	6	0.65	12.93
3/12	refilled gas	6	0.61	9.93
6/1	refilled gas	8	0.79	4.05
10/1	refilled gas	5	1.05	9.79
13/1	refilled gas	5.5	1.13	9.65

experiments and also the oxygen content found in herring by Fahlen (1967) may indicate that the vascular system or tissue surrounding the swimbladder are also a source of swimbladder gas.

If the gas in the swimbladder is deposited there only by swallowing or other injecting processes direct from the gaseous atmosphere, it means that the fish must be heavily overinflated at the surface in order to be buoyant at, e.g. 100 m depth. On the other hand the fish can have a gas volume which is able to keep them buoyant in the upper few meters and thereby be in negative buoyancy at any depth below that.

Herring may carry out extended vertical migrations, i.e. over pressure ranges up to 40 atmospheres. Herring in the present investigation caught at 10 m depth had a gas volume of 6 cc. If one assumes that the herring was buoyant at that depth, it must then take in another 458 cc of air at the surface to be buoyant at 400 m depth. Such a situation of the herring has so far not been observed in our investigations.

The other possibility is to keep the swimbladder volume constant by the rigidity of the swimbladder or the body wall. By using a transduser technique (Sundnes and Gytre 1972, in press), the pressure of the swimbladder gas in live herring was measured in relation to the surrounding hydrostatic pressure. The internal gas pressure of the herring followed the hydrostatic pressure on the outside. Whether minute pressure differences are possible in herring which are «cooperating» during the experiment is unknown, but it is clearly evident that no physical rigidity exists in the herring which can keep the swimbladder volume constant over those pressure ranges where herring perform vertical migrations. This means that only by access to atmospheric gases at the surface will herring not be buoyant in the major depth area of their distribution. Against this opinion numerous echo sounding observations of gas release indicate an overflotation of the herring from all depths when migration occurs toward decreasing hydrostatic pressure. At the surface this is also

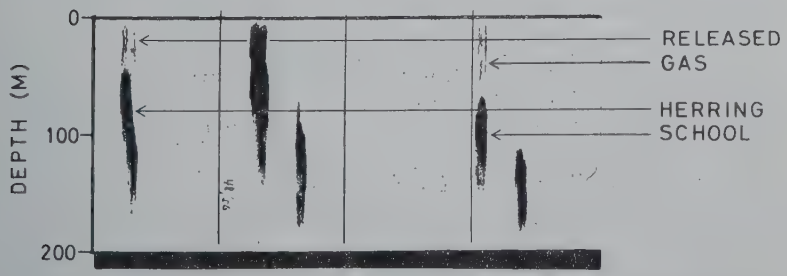

Fig. 1. Echogram showing gas release from migrating herring. (Photo: G. Vestnes).

visible by eye as previously described in the present chapter. In Fig. 1 gas release situation of herring is shown.

As previously discussed, buoyancy measurements of herring and char are problematic, but a few observations indicate that both species are buoyant at their depth of catch (Fig. 2).

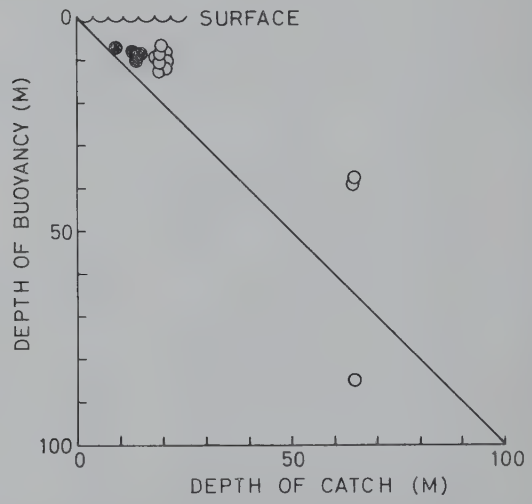

Fig. 2. Depth of buoyancy of *Clupea harengus* (●) and *Salmo alpinus* (○) in relation to depth of catch. The diagonal is the line of perfect buoyancy, i.e. where depth of buoyancy equals depth of catch.

The findings presented here indicate that both the herring and the char are able to compensate for the volume loss of the swimbladder due to hydrostatic pressure and without access to the surface.

Another question which is related to this type of swimbladder concerns their compressibility due to the effect of migration towards higher hydrostatic pressure as previously described. There are no indications that the herring compensate for the increased hydrostatic pressure as fast as the vertical migration takes place. As the swimbladder and its geometry are known to play an important part of the target strength in acoustical methods (McCartney and Stubbs 1971), further investigations must elucidate an eventual effect on the target strength of Clupeids and Salmonids due to vertical migration and during the restoration of neutral buoyancy at a certain depth.

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FECUNDITY AND EGG SIZE OF SPRING SPAWNING BARENTS SEA CAPELIN

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ABSTRACT

Gjøsæter, J. and Monstad, T. 1973. Fecundity and egg size of spring spawning Barents Sea capelin. *FiskDir. Skr. Ser. HavUnders.*, *16*: 98—104.

Fecundity of Barents Sea capelin was studied in 1971 and 1972. No differences were found between these two years. The regression line

$$\log F = 3.4871 \cdot \log L - 0.2049$$

was fitted to the whole material. This is in good accordance with studies on Barents Sea capelin carried out by others and shows much lower fecundity than capelin from New Foundland waters.

Diameters, measured on artifically fertilized eggs, ranged between 1.10 and 1.23 mm, mean 1.165 mm, and diameters of eggs from spawning beds measured between 1.10 and 1.20, mm mean 1.184 mm. Canadian and Icelandic measurements show smaller and similar sizes respectively.

INTRODUCTION

Spring spawning capelin, *Mallotus villosus* (Müller), from the Barents Sea mature at an age of 3 and 4 years and spawn from February to April along the coasts of northern Norway and Murman. Capelin are believed to be one time spawners, but parts of the stock probably survive and spawn one year later for a second time (Prokhorov 1965). Earlier work on fecundity of the Barents Sea capelin has been reviewed by Prokhorov (1965). Fecundity of capelin in Newfoundland waters has been studied by Templeman (1948) and Winters (1971). An extensive difference in egg numbers seems to occur between these two stocks of the North-Atlantic capelin. Diameters of fertilized eggs of Newfoundland capelin have been measured by Templeman (1948) and of Icelandic capelin by Fredriksson & Timmermann (1951). No comparable data is found for Barents Sea capelin, although Pozdnyakov (1967) has measured some ripe interovarial eggs.

This paper gives data on fecundity and egg size of Barents Sea spring spawning capelin for the years 1971 and 1972. The results of the present study are compared with data from Canada, U.S.S.R. and Iceland.

METHODS

Prespawning capelin were collected by pelagic trawl off Finnmark in February 1971 and 1972. Total length of the fish, i.e. the length between the anterior end of the mandible to the posterior end of the ventral lob of the caudal fin in natural position, was measured in 1971 on fresh material and in 1972 on frozen. To make the measurements comparable, shrinking due to freezing and thawing was adjusted for by using the equation

$$L_{fresh} = 1.01\ L_{frozen} + 0.273$$

developed by Monstad (1971). Length measurements made by Pozdnyakov (1957) were converted from fork length to total length by adding 8% (Templeman 1968). The age of the fish was determined from the otoliths.

In 1971 the gonads were removed from the fresh fish and placed in 10% formalin. In 1972 the fish were frozen, and after about one week the gonads were removed and transferred to formalin. As it turned out to be quite easy to separate the eggs of capelin gonads kept in formalin, Gilson's fluid was not used.

After separating the eggs from each other, a whirling vessel (Wiborg 1951) was used to fraction the samples, and one sample of 1/10 of both gonads combined was counted from each fish. A study of egg size was carried out in 1971. Eggs were artificially fertilized and kept in glass jars with sea water at 5°C for about 12 hours. Diameters of a hundred eggs or more from each fish were measured using a Watson eyepiece micrometer. Length and age of these fish were recorded.

Diameters were also measured on live eggs from natural spawning beds situated along the Finnmark coast.

RESULTS

FECUNDITY

In 1971 eggs were counted in 48 specimens ranging between 14.1 and 18.2 cm in length. Fecundity ranged between 5800 and 19090 eggs per female (Fig. 1). The following logaritmic regression of fecundity (F) on length (L in cm) was found:

$$\log F = 3.6473 \cdot \log L - 0.4074$$

In 1972 egg counts were made from 34 capelin ranging between 14.2—18.6 cm. Fecundity ranged from 5250 to 19070 eggs per female. Accordingly the regression line

$$\log F = 3.2508 \cdot \log L + 0.0924$$

was found.

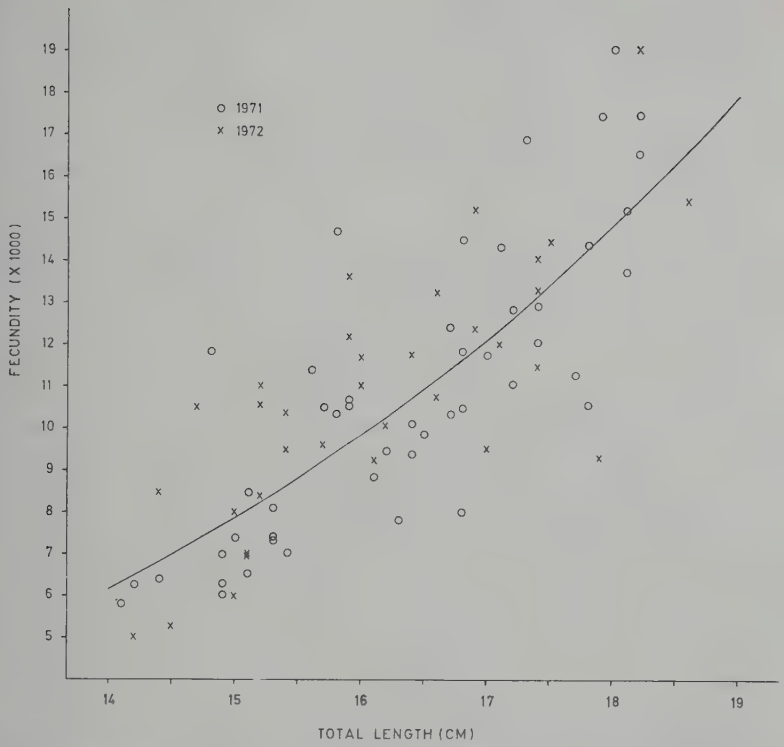

Fig. 1. Fecundity of Barents Sea capelin from 1971 and 1972 with the regression line $F = 0.3913 \cdot L^{3.4871}$

Correlation coefficients, r, variances of estimate, $S^2_{\log F \log L}$, regression coefficients, b, with confidence intervals, and intercepts, a, with confidence intervals are listed in Table 1. Both correlations are highly significant.

Values of t between the regression coefficients, b, and between the intercepts, a, for the years 1971 and 1972 are 0.358 and 0.040 respectively. This shows that there is no significant difference in fecundity-length relationship between the two years. Therefore the material from the two years were combined, and the regression line

$$\log F = 3.4871 \cdot \log L - 0.2049$$

was found. Some parameters for this regression are also listed in Table 1.

This equation can be converted to

$$F = 0.3913 \cdot L^{3.4871}$$

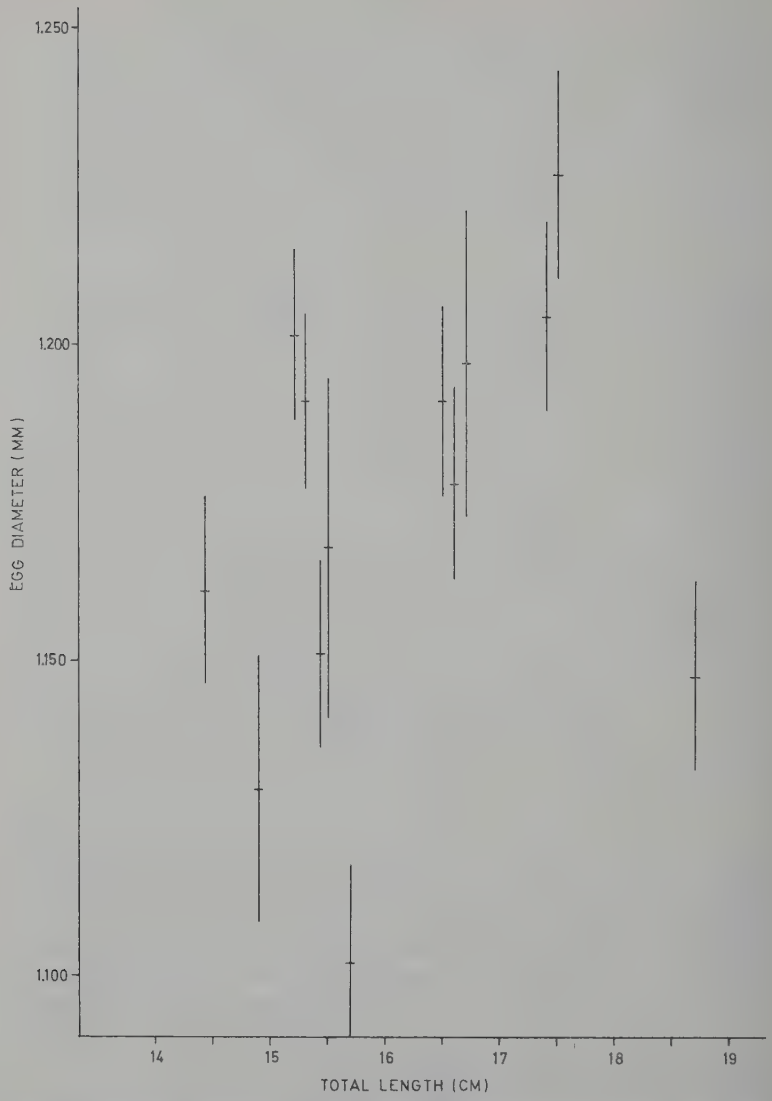

Fig. 2. Diameters of artificially fertilized eggs of Barents Sea capelin from 1971. The range of the vertical bars show two standard deviations.

Table 1. Parameters of the regression line $\log F = b \log L + a_n$ used for fecundity (F) and length (L) on Barents Sea capelin.

Year	n	b ± 95% conf.lim.	a ± 95% conf.lim.	r	$S^2 \log F \log L$
1971	48	3.6473 ± 1.4186	— 0.4074 ± 1.7174	0.82	0.023
1972	34	3.2508 ± 1.6283	+ 0.0924 ± 1.9626	0.75	0.021
Total	82	3.4871 ± 1.0420	— 0.2049 ± 1.0243	0.79	0.015

Monstad (1971) has shown that the length-weight relationship for maturing female Barents Sea capelin taken during late winter has the form

$$W = 0.00036 \cdot L^{3.89}$$

(W = weight in g, L = length in cm).

The conclusion, therefore, is that fecundity is changing nearly linearly with weight.

In the material analysed 72 specimens were 4 years old and only 8 and 2 were 3 and 5 years respectively. It is therefore impossible to analyse the effect of age on fecundity.

The results of the egg diameter measurements are shown in Fig. 2. The size of eggs varied between 1.10 and 1.23 mm, mean 1.165 mm. The regression line

$$D = 0.081 \cdot L + 1.040$$

of mean diameter of eggs, D (mm), on fish length, L (cm), was found. The results suggest that the diameter is increasing with fish length (Fig. 2), but the correlation coefficient $r = 0.2684$ shows that the correlation is not significant ($P > 0.05$).

In addition to artificially fertilized eggs, 467 live eggs from 3 spawning areas were measured. The following mean diameters were found: West-Finnmark, 1.177 mm (N = 147); Mid-Finnmark, 1.174 mm (N = 223); East-Finnmark, 1.218 mm (N = 97). Mean for the whole area was 1.184 mm.

DISCUSSION

Fecundity of Barents Sea capelin has been studied by Pozdnyakov (1957), who counted eggs from 128 specimens. Fecundity ranged from 4518 to 22021 with a mean of 10764 eggs, and the corresponding lengths were between 12.5 and 19.0 cm, mean 16.1 cm. No regression line was fitted but he suggested an almost linear relation between weight and fecundity.

Table 2. Mean lengths and fecundity from Pozdnyakov (1957) compared to fecundity at same lengths from the regression line log F = 3.487 · log L — 0.2049.

Length (cm)	Fecundity	
	Pozdnyakov	Authors
13,7	6 319	—
14,8	7 455	7 525
15,8	9 695	9 441
16,1	10 764	10 070
16,9	12 362	11 930
17,7	15 334	14 030
18,8	17 285	17 310

His data shows a slight, but insignificant higher fecundity than the present study (Table 2).

For Atlantic capelin in Canadian waters fecundity has been studied by Templeman (1948) and also by Winters (1971) who found the regression line

$$\log F = 2.94 \log L - 4.8473$$

indicating a higher fecundity than in the Barents Sea.

In capelin from the area off British Colombia, ranging in total length between 10.7 and 12.2 cm, Hart & Mchugh (1944) found a fecundity range of 3020—6670 eggs, mean 4590.

Because of the small size at maturity, a comparison of this data to ours is very difficult.

Diameters of fertilized eggs of Atlantic capelin from Canada have been measured by Templeman (1948). He found a mean diameter of 0.965 mm and the range from 0.901 to 1.037. His material was preserved in 10% formalin, but the developmental stage is not reported. The mean diameter of eggs from Barents Sea capelin were approximately 23% higher than this. Shrinkage of eggs in 4% formalin is about 7% (Hiemstra 1962) and cannot acount for the total difference. It can therefore be concluded that Barents Sea capelin have bigger eggs than Atlantic Canadian capelin. This is also to be expected from the differences in fecundity-length relationship between the two stocks.

In Icelandic capelin Fredriksson & Timmermann (1951) found diameters ranging between 0.98 and 1.27 mm with the mean 1.12 mm in fertilized eggs taken from a spawning bed. Preservation and developmental stages are not reported. Comparison is therefore difficult, but the eggs of Icelandic capelin seems to be of similar size as eggs from Barents Sea capelin.

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ESTIMATES OF STOCK SIZE AND REPRODUCTION OF THE BARENTS SEA CAPELIN IN 1970—1972.

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ABSTRACT

Dragesund, O., Gjøsæter, J. and Monstad, T. 1973. Estimates of stock size and reproduction of the Barents Sea capelin in 1970—1972. *FiskDir. Skr. Ser. HavUnders.*, *16*: 105—139.

The distribution and migration of young and maturing capelin during the period 1969—1972 have been investigated by combined acoustic surveys and fishing experiments.

The nursery area of the capelin is extensive, but the main grounds are in the central and eastern part of the Barents Sea. The two and three year old fish are distributed farther north and northeast than the younger capelin.

Previously, the main part of the spawning stock approached the western part of the Murman coast and the Varanger peninsula, and dispersed westward along the Norwegian coast. During recent years, a major part of the stock also reached the coast of West-Finnmark and migrated farther west and south along the coast for spawning.

The capelin mainly become sexually mature when they are four years old. A very heavy postspawning mortality is observed, and most likely very few capelin survive to spawn a second time.

At present the Barents Sea capelin is the most important fish resource for the Norwegian purse seine fleet, and Norway has been responsible for more than 90% of the total catch from this resource.

Preliminary spawning stock size estimates for 1971 and 1972 are available from acoustic surveys, egg and larval surveys, and tagging experiments.

It is tentatively concluded that the spawning stock size in 1971 was at a high level, being somewhat lower both in 1970 and 1972.

So far no sign of overfishing has been observed. The increase in catch during the last six years is due to a significantly increased fishing effort, but also for a larger part attributed to a raise in the stock size.

A more detailed analysis of the location and time of spawning during the 1971 season is given. Spawning took place along the coast from Vesterålen to Varangerfjord. The major spawning west of North Cape took place during March and off the coast of eastern Finnmark in April.

Fertilization and survival of eggs were studied. On the spawning beds the fertilization seemed to be almost 100%. Egg mortality seemed to be low. The distribution of capelin larvae, during the first month after hatching, was studied. The larvae were collected on five surveys in oblique hauls with Clarke Bumpus plankton samplers.

INTRODUCTION

The annual yields of the Norwegian capelin has gradually increased during the last two decades, and at present the Barents Sea capelin is the most important fish resource for the Norwegian purse seine fleet. Previously capelin were exploited commercially mainly during winter and spring when the mature stock enters coastal waters to spawn, but since 1968 an important fishery has also developed for capelin on the feeding grounds in the Barents Sea (Fig. 1). It is apparent from the history of the fisheries that great variations in spawning time and area have occurred, and that the stock strength has fluctuated widely (Olsen 1965, 1968). These fluctuations strongly influence the fisheries, and in 1960 the Institute of Marine Research started a programme of capelin investigations with the aim of establishing the causes of these fluctuations and if possible, making prognoses for the fishery.

Each year in February—March, and in later summer and autumn, research vessel surveys have been carried out in the Barents Sea (Møller og Olsen 1962, Olsen 1968, Monstad 1969, Lahn-Johannessen og Monstad 1970). The work has included sonar and echo sounder searching, sampling with midwater and bottom trawls, and hydrographic observations. Since the 1961 season, sampling of the commercial landings has been carried out, and records of biological data for the last decade are available.

Due to the increasing fishing effort, great attention has recently been given to the question of regulating the fisheries for the Barents Sea capelin. Thus in 1970 the Norwegian government introduced a time regulation by closing the summer season from 1 June to 15 July. In 1971 it was prohibited to land catches of capelin from 15 May to 24 July and in 1972 from 1 May to 24 July. A minimum legal size of 12 cm was set in 1971. For the 1972 season it was recommended to increase the minimum size to 14 cm, in order to utilize the growth potential of the young fish (Dragesund, Monstad og Ulltang 1973). However, the decision was taken by the Government to increase the legal minimum size by only 1 cm.

The need for regulatory measures during the spawning season has also been discussed. The question has arisen as to whether the intensified fishery during the years 1970—1972 has endangered the future reproduction of the stock. During the winter fishery of 1972 the season was closed for a short period from 19 to 26 March west of North Cape and from 27 March to 9 April east of North Cape.

In order to give more reliable prognoses for the fishery and to collect adequate material for regulatory measures to be taken, the Norwegian

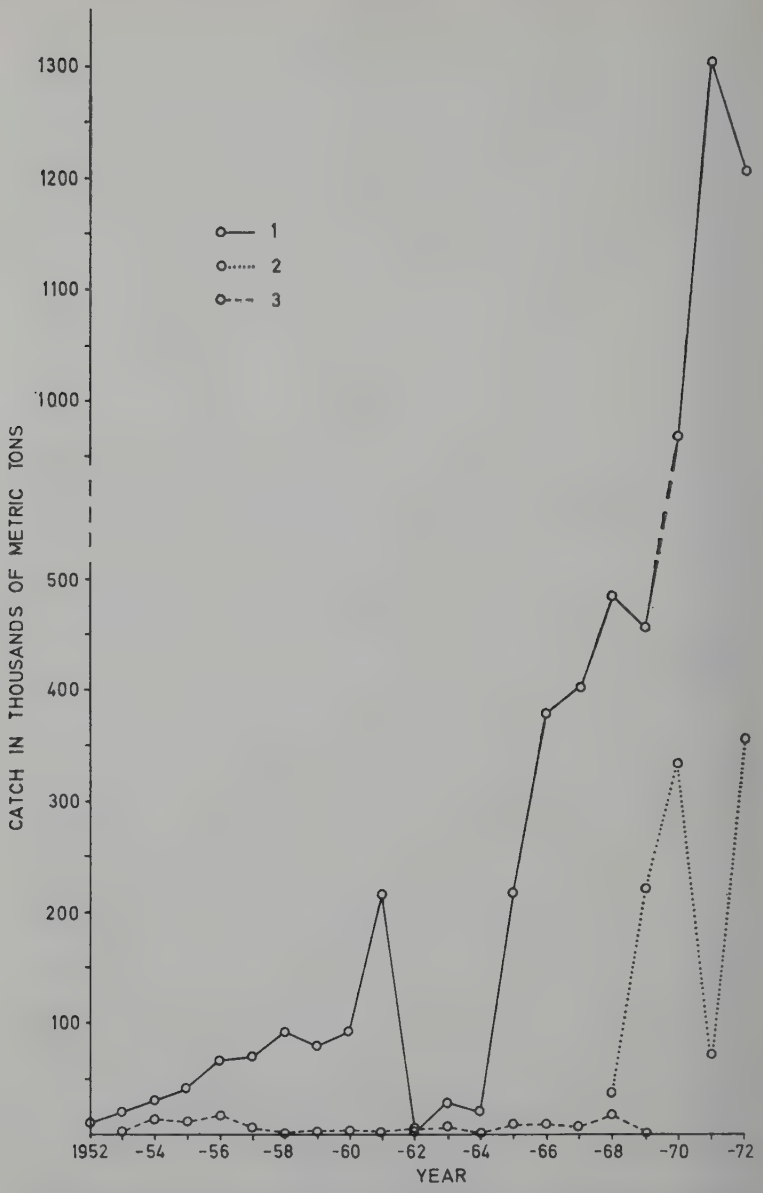

Fig. 1. Catches of Barents Sea capelin in 1950—1972. 1) Norwegian winter fishery, 2) Norwegian summer fishery, 3) Soviet winter- and summer fishery.

capelin investigations were considerably extended in 1971 by including more qualitative work on the Barents Sea capelin resource and its production of recruits.

The aim of the present paper is to report some results of the investigations carried out the last three years with emphasis on:

1) distribution and migration of capelin during autumn and winter;
2) structure and size of the spawning stock;
3) reproduction of the stock and the resulting year-class strength.

MATERIAL AND METHODS

Most of the material is obtained from investigations carried out during autumn and winter 1969—1970 to 1971—1972. It includes data from acoustic surveys, egg and larval surveys, tagging experiments, samples of capelin and catch statistics.

ACOUSTIC SURVEYS

Every autumn, during October to December, the distribution and abundance of adult capelin in the Barents Sea were studied from combined acoustic surveys and fishing experiments with pelagic trawl (Monstad 1971, Jakupsstovu *et al.* 1972). Similar acoustic surveys were conducted from January to late February (Lahn-Johannessen og Monstad 1970, Blindheim og Monstad 1972). In 1971 and 1972 investigations were also carried out during the spawning season from mid-March to the end of April. In order to give a more quantitative distribution of the capelin resource, special echo surveys were undertaken in August-September 1970 and 1971 (Blindheim *et al.* 1971, Dragesund og Nakken 1972).

The research vessels used («Johan Hjort» and «G. O. Sars») were equipped with vertical echo sounders, echo integrators and horizontal ranging sonars, and during the surveys the acoustic instruments were operated continuously. The settings of the Simrad echo integrator and the EK 38 kHz echo sounder during the surveys in August-September 1970 and 1971 were: Output power 1/10 effect, time varied gain (TVG) 20 log R and receiver gain — 20 dB. The source level was 136 dB, receiving voltage response 7.8 and the beamwith 5° and 5.5° along and athwartship between the 3 dB points. In order to avoid saturation of the echo integrator the gain was adjusted when necessary. Three echo integrators with six echo integrator channels were used, each covering a depth interval of 50 m. Echo integrator readings were made each

nautical mile, and average values of each five miles were plotted on maps.

When other fish species were recorded within the same depth interval, the echo abundance was divided between capelin and the other species. Both experimental fishing and analysis of the echo traces were used for diving the total echo abundance (Blindheim *et al.* 1971).

A method to estimate the stock size based on acoustic surveys, is developed by Midttun and Nakken (1971), Blindheim and Nakken (1971) and applied by Midttun and Nakken (1972).

The total echo abundace (T) was estimated from the equation

$$T = \int_A \varrho \, dA \tag{1}$$

where A is the area of distribution and ϱ the number of fish or fish weight per unit area.

C is calculated from the relation of Midttun and Nakken (1971),

$$\varrho = C\,M \tag{2}$$

where C is approximately constant for the same species in case ϱ is measured in fish weight per unit area. M is the integrated echo intensity. The procedure for calculating C is described by Blindheim and Nakken (1971).

Applying (1) and (2) $T = C \int_A M dA$ (3)

$$T = C_{T\ relative} \tag{4}$$

where $T_{relative}$ has the dimension: mm echo integrator readings $\times$ unit surface area.

By integrating the area between the isolines on the map where the echo integrator readings are plotted, $T_{relative}$ can be found.

EGG AND LARVAL SURVEYS

During surveys carried out in winter of 1971 and 1972, capelin eggs were collected by Pettersen grab, but were also sampled by diving and from the stomach content of haddock, cod and saithe caught by bottom trawl. A more detailed description of the diving technique used is given by Bakke and Bjørke (1973).

The larvae were collected in oblique hauls with Clarke—Bumpus plankton samplers (CBPS). The length of the nylon net used was 60 cm with a mesh size of 0.5 mm. The CBPS were equipped with flowmeters, and three samplers were towed simultaneously at different depths and raised in 5 m steps.

The sampling depths were 25—5, 50—30 and 75—55 m. The total towing time was 20 minutes. A weight of 28 kg was attached at the end of the 4 mm thick wire which was kept as close as possible to an angle

of 50° from the surface by keeping the towing speed between 1.5 and 2.0 knots. Because of difficulties in operating the closing mechanism of the CBPS in bad weather, this was permanently kept in open position. The number of larvae collected was converted to numbers below 1 m^2 sea surface.

In order to evaluate the size of the spawning stock, the total number of eggs in a locality near North Cape (Nordvågen) was estimated in 1971. One week after hatching commenced, a detailed larval survey was carried out in the area where larvae from Nordvågen were distributed. Probably some larvae had drifted out of the area, and some larvae from other spawning grounds may have drifted into it; though it is belived that the estimated number is reasonably close to the real one. The ratio, between eggs spawned in Nordvågen and the number of larvae derived from these eggs and available to the plankton gears during the given period of time, was calculated. This ratio between eggs and larvae can be applied to the whole spawning area, provided that:

1) the plankton samplers are taken at the same time in relation to the hatching sequence;
2) that hatching success and mortality of the implied larval stages are the same in all areas, or that the area selected for the detail study has conditions corresponding to an average for the other areas;
3) the larvae sampled are equally representative in all areas.

By this method number of eggs spawned can be computed from number of larvae taken during a larval survey, and when fecundity is known, number of fish which have spawned can be found. A more detailed discussion of this method is given by Gjøsæter and Sætre (1973).

TAGGING EXPERIMENTS

During the winter seasons of 1971 and 1972 tagging experiments were carried out from the scouting vessel «M. Ytterstad», which on this occasion was equipped with purse seine. The capelin were tagged with internal steel tags measuring 14 × 3 × 0.5 mm. A tagging device, especially developed for inserting this tag, was used. After being carefully brought from the purse seine into the tank on deck, the capelin were taken out indicidually, imidiately tagged, and were released in batches of approximately 20 individuals into the sea by means of a bucket.

Nearly all tags recovered were found at Norwegian reduction plants where magnets are installed for detecting the tags. The efficiency of the

magnets was tested during the winter seasons of 1971 and 1972. The procedure for testing the magnets, and the routine for collecting data on the catches and tags recovered at Norwegian reduction plants, are described by Aasen (1958) and by Dragesund and Haraldsvik (1968).

The spawning stock (S) was estimated from the relation

$$S = \frac{S_1 \cdot N_1 + S_2 \cdot N_2 + \text{- - - - - - - - - - } S_n \cdot N_n}{N} \quad (5)$$

where S_1, S_2 - - - - - - - S_n are the stock sizes estimated from each release and N_1, N_2 - - - - - - - N_n the number of tagged fish. N is the total number of tagged fish. S_1, S_2 - - - - - - - S_n are estimated from the relation

$$S_n = \frac{N_n \cdot C_n \cdot s}{R_n} \quad (6)$$

where C_n is the catch subesequent to the n^{th} release and R_n the number of recaptures from this release.

s is the tagging survival, taking into account both tagging mortality and shedding of tags. No decisive experiments on capelin have been carried out on tagging survival with internal steel tags. This factor certainly plays an important role in the calculations of the stock strength and has to be adjusted for. Tentatively s is set to 0.80.

CAPELIN SAMPLES AND CATCH STATISTICS

During the acoustic surveys capelin were caught with a Norwegian capelin trawl with an opening of 12 × 12 fathomes, mesh size (stretched) ranging from 200 mm (wings and squares) graded down to 22 mm (cod end). An ordinary Granton bottom trawl with cover net equipped with bobbins was also available.

In addition to samples collected during the acoustic surveys, capelin samples were collected throughout the winter seasons of 1970—1972 from commercial catches. The capelin were examined fresh or from frozen material.

Total length was measured to the nearest mm and grouped in half cm class intervals (Gjøsæter and Monstad 1973). Otoliths, mainly taken stratified, were used for age determination, and age-length keys were established. The maturity stages were classified according to a scale used by Monstad (1971). The weigth in g was recorded.

During surveys the volume of individual fish was measured by the displacement method, and from this the weight was estimated.

Catch statistics of the Norwegian landings were obtained from the official fishery statistics. Statistical information, on the geographical distribution of commercial catches of spawning and spent capelin in

winter 1971, was supplied from the fishermen's sales organization, Feitsildfiskernes Salgslag. Statistics of landings by USSR were derived from «Bulletin Statistique des Peches Maritimes».

DISTRIBUTION AND MIGRATION

The distribution of capelin in August—September 1970 and 1971 is illustrated in Fig. 2, 3 and 4. The survey in 1970 did not cover the area east of 40°E and north of 77°N. In the western part of the investigated area the abundance was significantly higher in 1970 (Fig. 2) than in 1971 (Fig. 3). During the second survey in 1971 (Fig. 4) the capelin were recorded somewhat farther west and north. The summer fishery on two and three years old capelin in 1969—1971 took place in this area, i. e. between 74°—78°N and 25°—45°E.

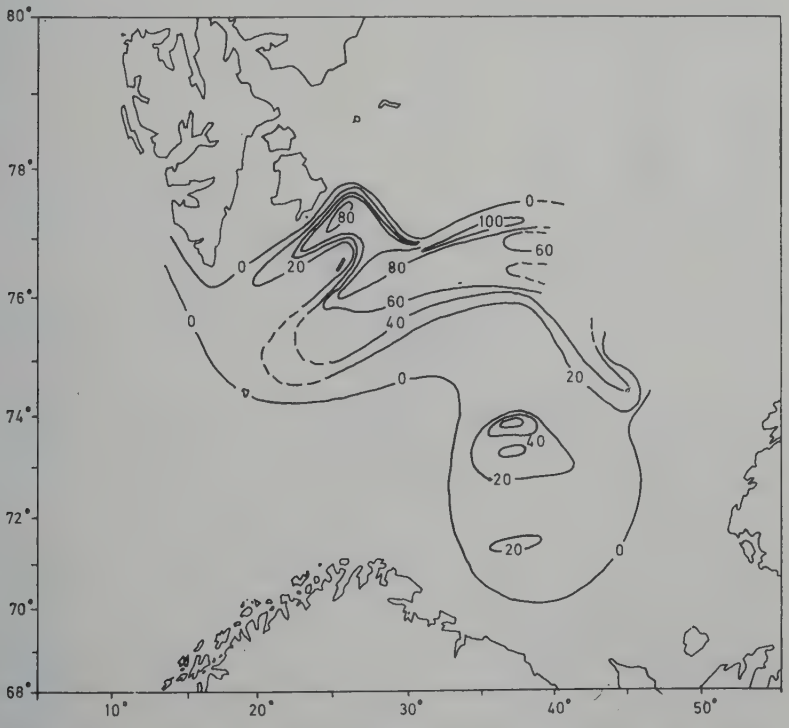

Fig. 2. Distribution of capelin 28 August—11 September 1970. Isolines and numbers are fish density as echo integtorar recordings in mm.

Fig. 5—7 show the distribution and migration during the prespawning period in 1969—1970, 1970—1971 and 1971—1972. In late autumn the maturing capelin segregate from the immature stock and gradually start their migration southward along the front between the cold and warmer water in the area from the Central Bank (75°N, 35°E) towards the Thor Iversen Bank (73°N, 35°E). From this region part of the stock moves farther south and southeast, whereas another component start migrating westward.

In previous years the main part of the spawning stock usully aproached the western part of the Murman coast and the Varanger peninsula and dispersed westward along the Norwegian coast (Prokhorov 1965, Møller og Olsen 1962). During the spawning seasons in 1970—1972

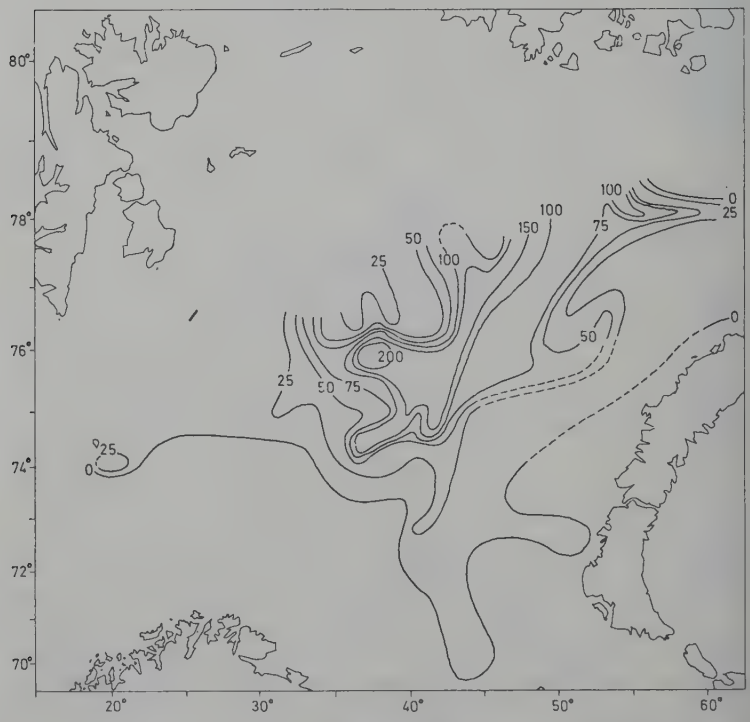

Fig. 3. Distribution of capelin 23 August—9 September 1971. Isolines and numbers are fish density as echo integrator recordings in mm.

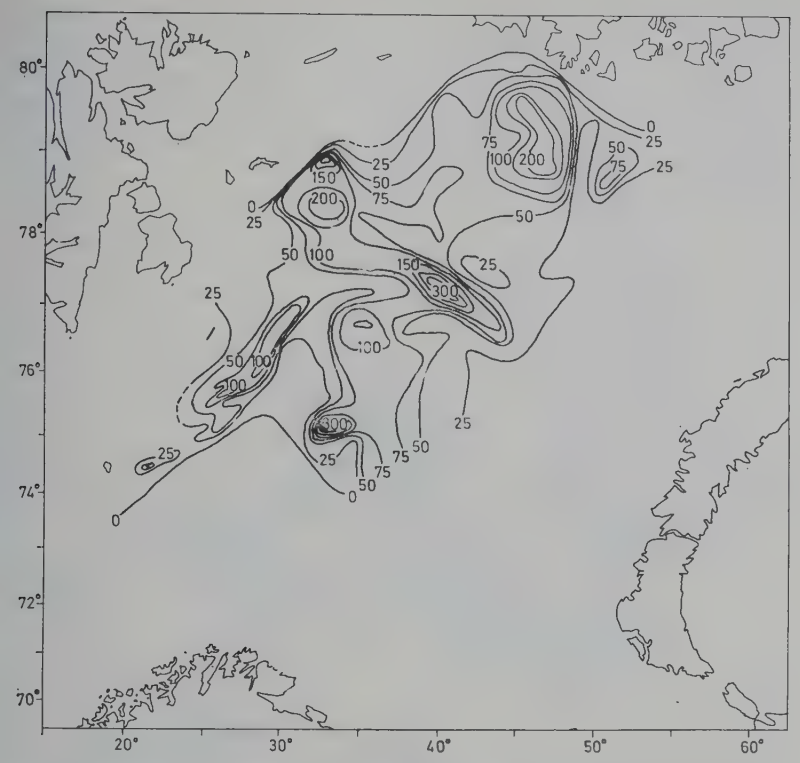

Fig. 4. Distribution of capelin 12—29 September 1971. Isolines and numbers are fish density as echo integrator recordings in mm.

as well as in 1968 and 1969 (Olsen 1968, Lahn-Johannessen og Monstad 1970) part of the stock also migrated from the open sea towards the coast of West-Finnmark (west of North Cape). The main part of the western stock component approached the coast between Sørøya and the North Cape during February. In 1970 the main part of the spawning stock was distributed east of North Cape where the most important fishery took place (Table 1). However, in 1971 mature capelin continuously approached the coast west of North Cape during February and March and dispersed farther west and south along the coast. In March concentrations of capelin were located off Senja and in March—April off Vesterålen. This is the most southern area of capelin catches recorded in Norwegian waters during the last two decades. Components of the stock also reached the Finnmark coast east of North Cape, but in contrast to previous years no great concentrations were observed along

the coast of eastern Finnmark in 1971, although the larval surveys indicated heavy spawning also in this area. The most important fishing took place west of North Cape, but profitable catches were also obtained east of North Cape. Also in 1972 most of the fishing took place west of North Cape, but the capelin did not move to the spawning grounds off Senja and Vesterålen.

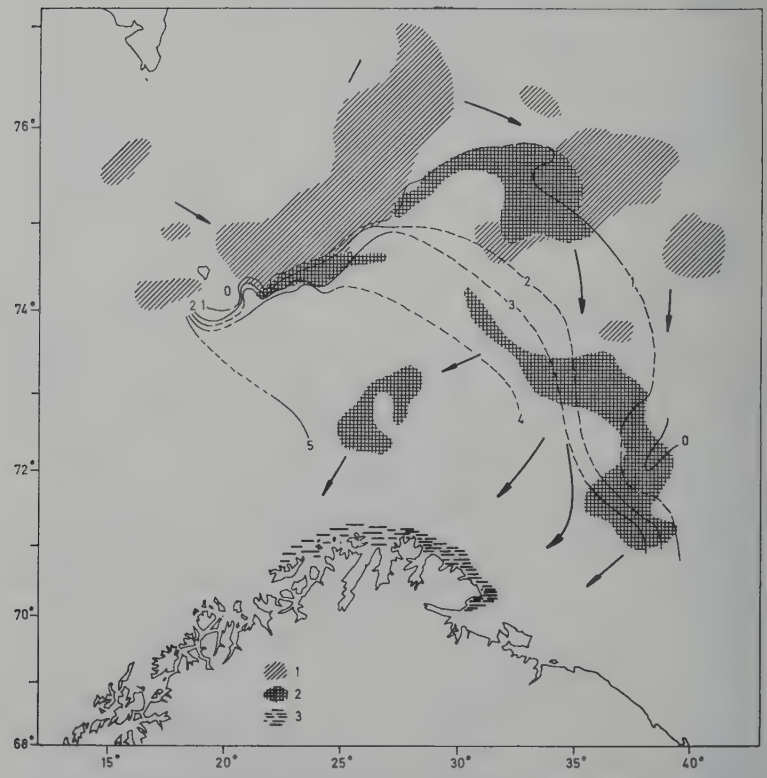

Fig. 5. Distribution of capelin during autumn and winter of 1969—1970. The temperature (°C) at 50 m depth in January 1970 is also indicated. Arrows denote the main migration routes. 1) October—November 1969, 2) January 1970, 3) March—April 1970.

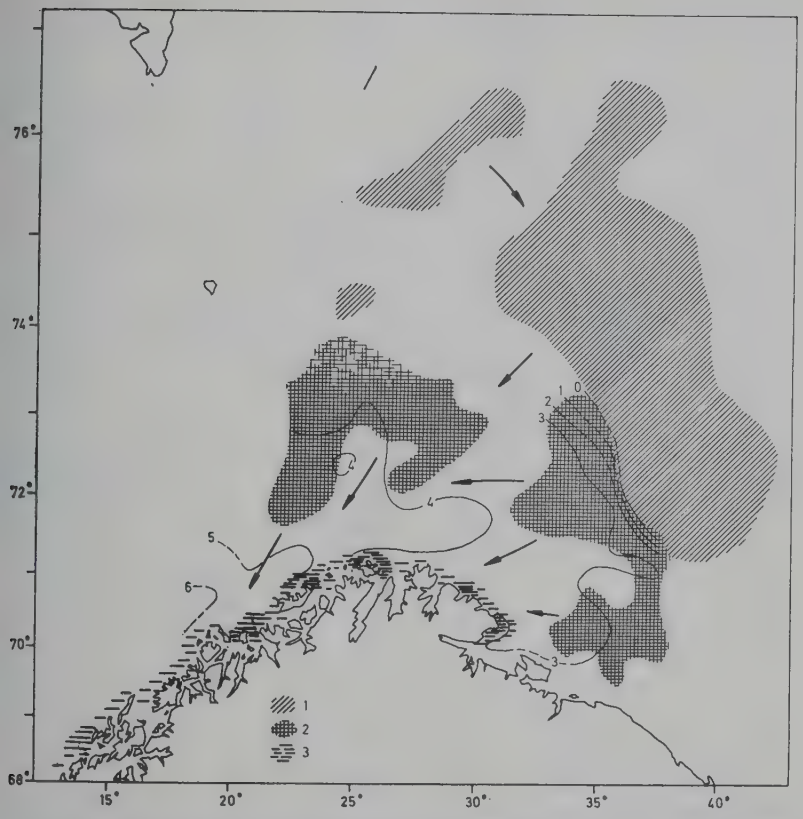

Fig. 6. Distribution of capelin during autumn and winter of 1970—1971. The temperature (°C) at 50 m depth in January—February 1971 is also indicated. Arrows denote the main migration routes. 1) November—December 1970, 2) January—February 1971, 3) March—April 1971.

Table 1. Catch of capelin (in thousand tons) during the winter seasons 1970—1972 west and east of North Cape respectively.

Month	Week no.	Year					
		1970		1971		1972	
		West	East	West	East	West	East
	3			7.035		71.630	
January	4		1.451	47.193	1.410	130.600	
	5	8.859	11.167	58.647		85.565	
	6	0.198	0.042	6.604	22.390	158.065	
	7	23.632	14.043	100.573	39.340	126.220	
February	8	88.283	10.210	101.555	42.909	69.931	
	9	95.381	35.295	127.950		52.607	0.100
	10	6.286	114.983	124.365	2.000	206.167	2.817
	11	31.065	95.023	117.710	19.010	147.240	
March	12	7.949	89.701	115.100	9.100	65.316	18.546
	13	2.558	67.702	142.508	20.636		105.330
	14	0.999	96.772	112.877	22.022	1.545	
	15		116.072	32.867	0.307		
April	16		31.070	5.649	31.925		
	17		7.255		5.060		
	18		0.131				
	19	0.023	0.544				
May	20		0.136				
	21						
	22		0.013				
Total		265.233	691.610	1 100.633	216.109	1 114.886	126.793

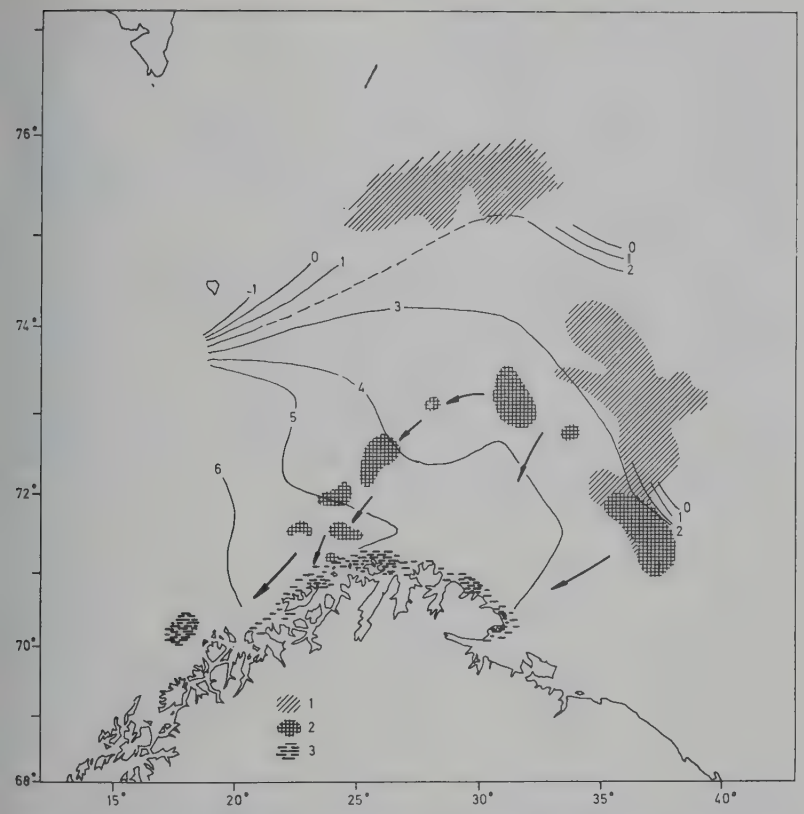

Fig. 7. Distribution of capelin during autumn and winter of 1971—1972. The temperature (°C) at 50 m depth in January—February 1972 is also indicated. Arrows denote the main migration routes. 1) November—December 1971, 2) January—February 1972, 3) March—April 1972.

STRUCTURE AND SIZE OF SPAWNING STOCK

The Barents Sea capelin spawn mainly when three and four years old, and the lack of older fish strongly supports the theory of a very heavy postspawning mortality. At the end of the spawning season dead and dying capelin were observed over wide areas. Possibly some capelin do survive to spawn a second time (Templeman 1948, Prokhorov 1965, Vilhjálmsson 1968, Winters 1971), but it is suggested that most of them die after spawning.

According to previous investigations, the major part of a year-class spawn at an age of four years (Olsen 1965, 1968, Prokhorov 1965). During the winter fishery in 1970 the rich 1966 year-class dominated the catches (Fig. 8), followed by the 1967 year-class.

Investigations carried out during the summer of 1970 (Blindheim *et al.* 1971) indicated that the 1967 year-class was rich, and during the winter season of 1971 this year-class showed to be very abundant and strongly dominated the catches (Fig. 9).

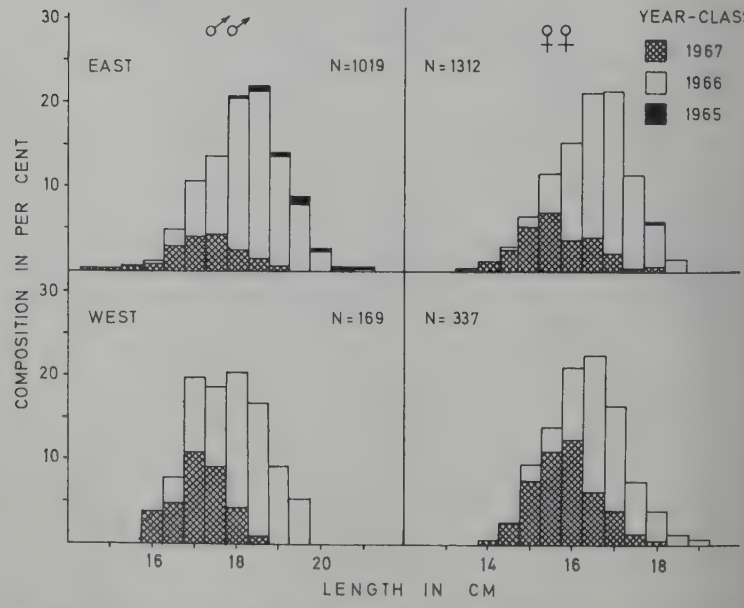

Fig. 8. Age and length composition of capelin during the winter season 1970 off eastern (East) and western (West) Finnmark.

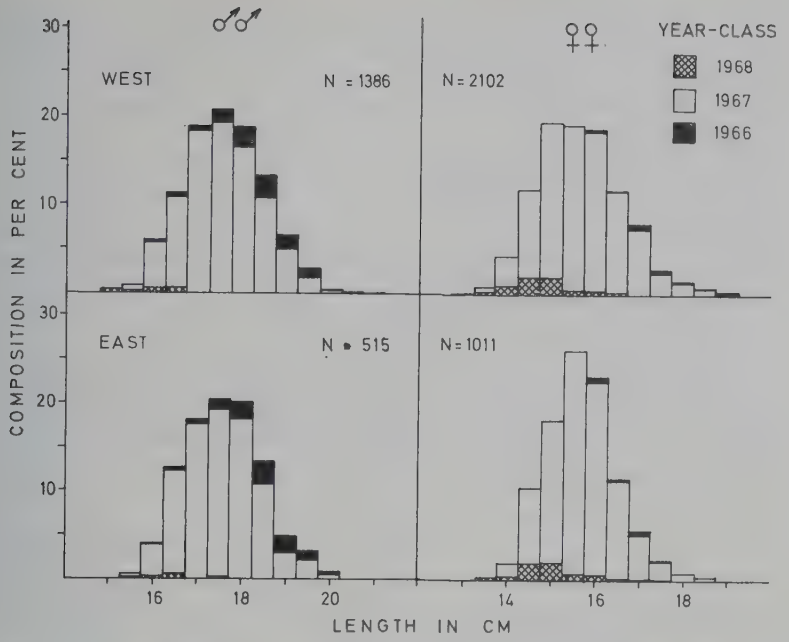

Fig. 9. Age and length composition of capelin during the winter season 1971 off western (West) and eastern (East) Finnmark.

Also, in the winter season of 1972 the four year old fish (1968 year-class) predominated (Fig. 10).

Estimates of the spawning stock size in 1971 are available from tag returns and data on egg and larval abundance and distribution, and for the 1972 season from tagging experiments and acoustic surveys. the different methods used are subject to great errors and will only give some indication of the order of magnitude of the stock size.

The tagging experiments both in 1971 and 1972 were carried out at the beginning of the winter season. The within season returns are listed in Table 2 and 3. The effective quantities of capelin processed during the season, at reduction plants equipped with tested magnets, are also given in Table 2 and 3. The effective quantity processed, subsequent to each release, was estimated according to date on weekly landings during the season (Table 1).

Applying relations (5) and (6), the stock size in 1971 was estimated to be about 5.9 mill. tons, and in 1972 to about 4.8 mill. tons. The

figures obtained from this method are overestimated and must be interpreted with caution. An estimate of the stock strength based on these data is only tentative due to lack of information on tagging survival, and because the number of returns are too low and probably not evenly distributed in the catches.

A preliminary estimate of the spawning stock size for the season of 1971 is also obtained from egg and larval surveys. On 7—9 May a detailed larval survey was carried out in the area where larvae from Nordvågen were distributed. Approximately 4×10^{10} larvae were present. Number of eggs spawned in Nordvågen was 7.5×10^{11}. Number of larvae in this period was therefore approximately 1/20 of the number of eggs.

The survey of the whole area and the detail survey should be conducted at the same time in relation to the hatching curve. This requirement is best solved if the survey between 2 and 17 June is selected (Fig. 18). This survey indicate that 1.5×10^{13} larvae were present, and

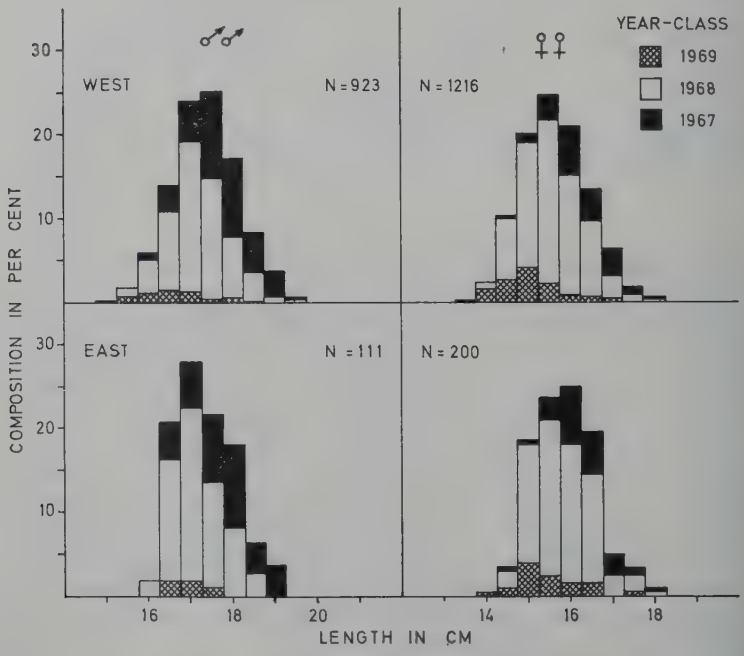

Fig. 10. Age and length composition of capelin during the winter season 1972 off western (West) and eastern (East) Finnmark.

Table 2. Quantity of processed capelin (tons) and number of returns from tagging experiments off the Finnmark coast during the winter season 1971.

Factory no.	Efficiency (e)	Quantity processed (p)	Corrected quantity (e . p)	Date and number of released capelin			
				16—18 February	24 February	11—12 March	Total
				3000	500	1500	
79.....	0.53	104 305	55 281	4	3	25	32
70.....	0.65	38 150	24 797	4		2	6
69.....	0.62	36 000	22 320	5			5
95.....	0.89	47 363	42 153	10	2	3	15
66.....	0.64	21 753	13 922	7		3	10
55.....	0.94	28 774	27 047	5		6	11
45.....	0.76	28 037	21 308	10			10
43.....	0.77	34 828	26 817	4		2	6
40.....	0.50	21 340	10 670	6			6
42.....	0.90	53 948	48 553	15		1	16
37.....	0.67	32 000	21 440	31			31
24.....	0.66	35 978	23 745	10	2	2	14
31.....	0.88	25 449	22 395	4			4
68.....	0.89	59 510	52 963	36	4	3	43
73.....	0.41	36 642	15 023			7	7
			428 434	151	11	54	216

accordingly that 3×10^{14} eggs had been laid. Assuming a mean fecundity of 10 000 eggs pr. female (GJØSÆTER and MONSTAD 1973), that males and females were present in equal proportions and that there are 3000 capelin in one hl, this corresponds to about 2.0 mill. tons of spawning capelin. Most of the capelin caught during the winter season were in the prespawning stage, and only between one and two hundred thousand tons of the total landings were spent capelin. The stock size at the beginning of the season, estimated from this method, should at least be in the order of 3.2 mill. tons.

A slightly different method, considering only number of young larvae, was applied by GJØSÆTER and SÆTRE (1973). This method indicated a spawning stock size in 1971 of 4.0 mill. tons.

The total echo abundance of capelin during the autumn of 1971 was estimated on the basis of the echo survey carried out 12—29 September (Fig. 4). Both immature and maturing capelin were distributed within the area surveyed (Fig. 11). The mean weight in the samples collected, showed that the maturing capelin made up 36% (weight) of the total stock. The total stock in the area surveyed was estimated from relations (3) and (4).

Table 3. Quantity of processed capelin (tons) and number of returns from tagging experiments off the Finnmark coast during the winter season 1972.

Factory no.	Efficiency (e)	Quantity (p)	Corrected quantity (e . p)	Date and number of released capelin				Total
				2 February	3 February	6 February	7 February	
				1200	1100	1500	300	
79	0.86	126 833	109 077	2	13	15	3	33
70	0.65	37 506	24 379	1	2	7		10
69	0.79	38 796	30 649	3	5	1		9
95	0.85	43 753	37 190	8	5	13	4	30
66	0.97	22 923	22 235	3	6	5		14
55	0.94	30 312	28 493	7	9	4	2	22
45	0.82	30 047	24 638	3	12	9	1	25
43	0.60	24 828	20 896		4	1	1	6
40	0.81	17 591	14 249	2	10	4		16
42	0.56	55 319	30 978	3	13	4	2	22
37	0.50	19 145	9 573	1	2			3
24	0.93	28 823	26 806	1	2	6	1	10
68	0.86	53 231	45 779	7	8	4	2	22
35	0.58	24 577	14 255	2		1	4	7
47	0.58	28 192	16 351	2	5	1	1	9
52	0.92	22 372	20 583	2	4	9	2	17
53	0.90	18 550	16 695	1	3	2	1	7
49	0.86	14 949	12 856	1	2	5	1	9
59	0.53	16 632	8 815		4			4
63	0.74	19 258	14 251			3	1	4
			528 748	49	109	94	26	278

$T_{relative} = 479 \cdot 10^4$ mm · (nautical miles)^2

$C = 2.1$ tons/mm · (nautical miles)^2.

The total stock of capelin (T) in the area was estimated to

$T = 10.1 \cdot 10^6$ tons

Assuming that all the maturing capelin migrated towards the coast for spawning in 1972, the size of the maturing stock was estimated to be between 2 and 3.6 mill. tons. This is a significantly lower figure than that obtained from tag returns (4.8 mill. tons). It is tentatively concluded that the figure estimated on the basis of the acoustic surveys is the most reliable of the two. It should be noted that the C probably is too high, and consequently this will result in an overestimation of the stock size (Midttun and Nakken 1972).

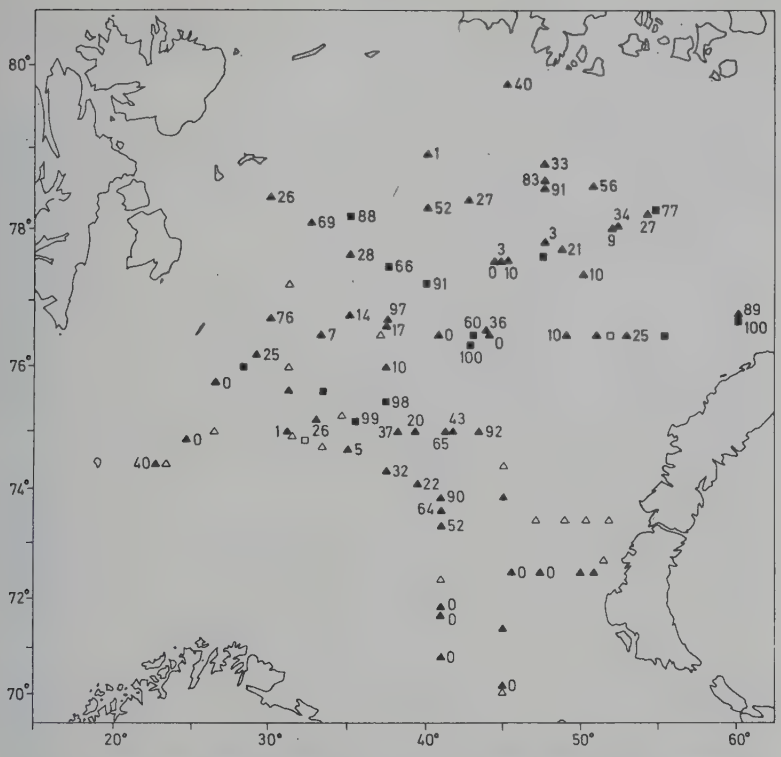

Fig. 11. Weight percentage of capelin $\geq$ 14 cm at each trawl station August—September 1971. Open symbols indicate no catch. At stations where the symbols are filled and no figure is given, only a few fish were caught, and no percentage is given. Triangles indicate pelagic — and squares bottom trawl stations.

REPRODUCTION AND RESULTING YEAR-CLASS STRENGTH

LOCATION AND TIME SPAWNING

To locate spawning concentrations of capelin in 1971 an echo survey was carried out during the second half of March (Fig. 12). The geographical distribution of commercial catches of spawning and spent capelin were compared with the echo integrator readings, and from these data a series of possible spawning places were found.

To verify the spawning, a grab station survey was carried out. Most of the stations were made in areas where capelin had been recorded. In some cases, divers were also used to locate spawning places (Bakke and Bjørke 1973). Eggs were found at 55 out of 227 grab stations. At 33 of these, eggs only occurred in numbers between 1 and 10 in each sample, indicating that the main spawning beds were surrounded by relatively large areas with small concentrations of eggs. This feature was also confirmed by the divers.

It is therefore suggested that, in areas where concentrations of eggs were sparse, mass spawning had taken place in a nearby area. The spawning places, found by grab or divers or both, are shown in Fig. 12.

The bottom substratum and number of eggs in the grab samples are shown in Table 4. Gravel was by far the most preferred substratum, and only few eggs were found on other substrata. The gravel on most spawning grounds had a grain size between 0.5 and 1.5 cm. Depth distribution of the eggs is shown in Table 5. Great concentrations of eggs were found to a depth of 65 m, while small numbers were observed

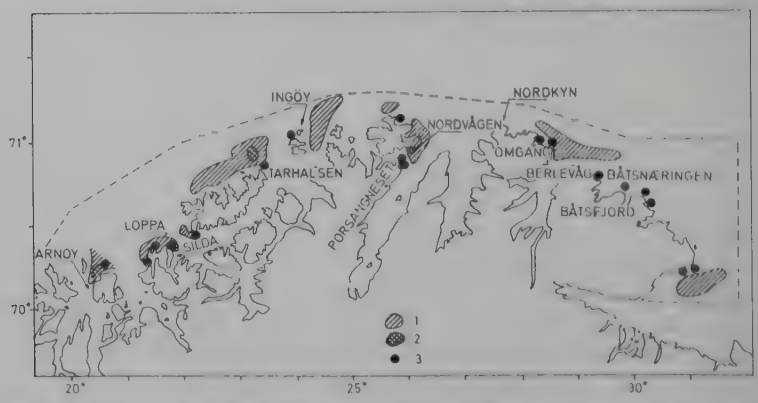

Fig. 12. Distribution of capelin 19—31 March 1971 and observed spawning places. 1) 1—10 integrator units, 2) > 10 integrator units, 3) spawning places.

Table 4. Substratum and egg density on the grab stations.

Substratum	Number of stations	No eggs	Scattered	Dense	Very dense
Gravel	28	11	2	10	5
Shell sand, shell fragments	44	29	10	4	1
Mineral sand	33	21	11	1	
Rocks, algae	117	106	10	1	
Silt, clay	5	5			

Table 5. Depth (in m) and egg density on the grab stations.

Depth	Number of stations	No eggs	Scattered	Dense	Very dense
10—19	36	19	5	9	3
20—29	45	34	9	2	
30—39	60	50	7	2	1
40—49	33	22	8	2	1
50—59	19	16	3		
60—69	9	8			1
70—79	9	7	1	1	
80—89	3	3			
90—99	4	4			
> 100	9	9			

to 75 m depth. The most shallow spawning beds were found at 12—15 m depth. Probably the bottom substratum is a more important factor for the location of spawning than the depth.

Both direct observations and study of the character of the substrtaum indicate a strong current at most of the spawning grounds.

The greatest concentrations of eggs were found at Loppa, Nordvågen and Båtsnæringen (Fig. 12). At Nordvågen egg densities of up to 8 mill. per m^2 were recorded in a local patch. However, most samples indicated egg densities between 1 and 3 mill. eggs per m^2. Similar great densities might also have been situated in other areas where only samples from the fringe or the surroundings of the spawning beds were taken.

Nordvågen was selected for a more detailed study. For this area a Decca map in scale 1 : 10 000 was made by reading the values of the decca meters. Simultaneously the position was determined by taking the bearing of selected land points (Fig. 13). The area was surveyed by grabbing, and all stations were plotted on the map. These stations were

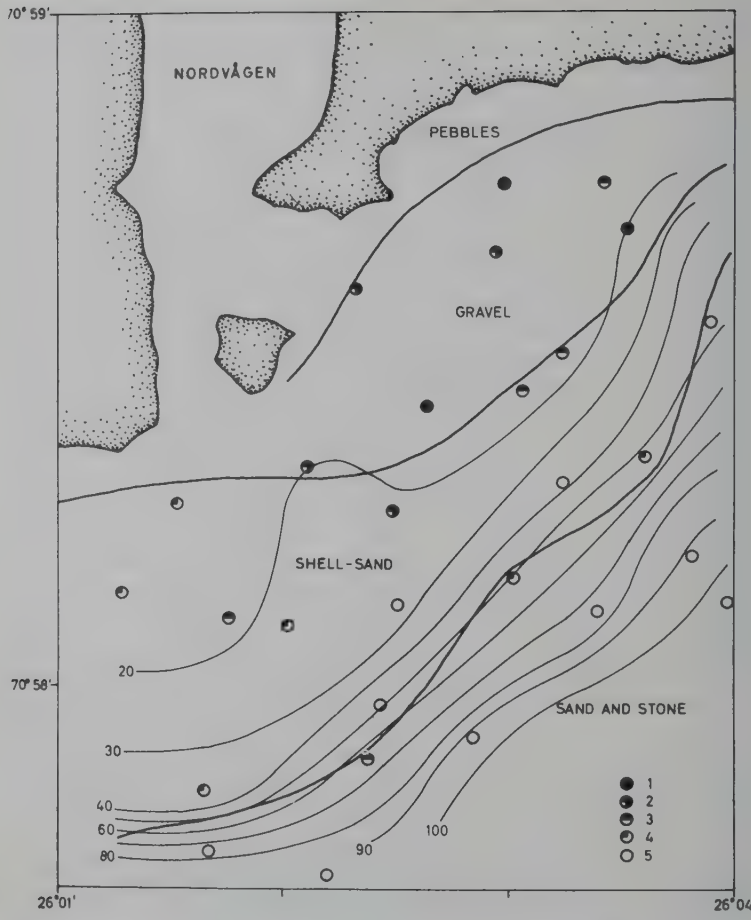

Fig. 13. Depth, bottom substratum and distribution of capelin eggs in Nordvågen 26 April 1971. 1) very dense, 2) dense, 3) scattered, 4) very scattered, 5) none.

later used for determining the area of the spawning bed. Divers were also used in this surveying.

The extension of the spawning bed in Nordvågen was about 0.2 km^2. This turned out to be very similar to the extension of the area with gravel bottom. Within this area a mean egg density of 2.5 mill. per m^2 was observed. A total of 7.5×10^{11} eggs had therefore been spawned

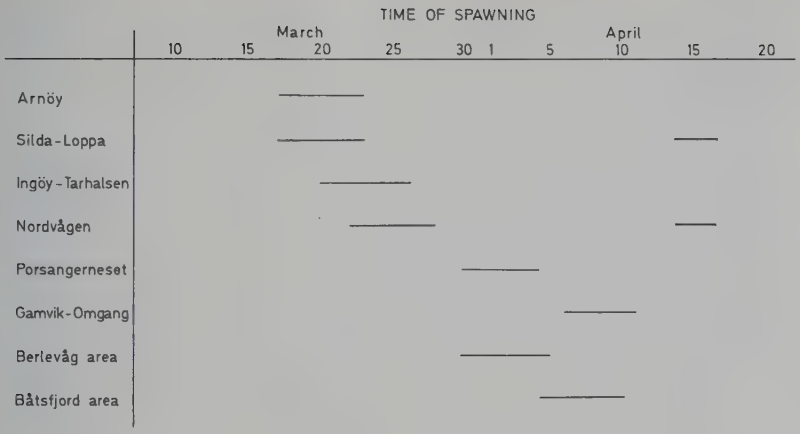

Fig.14. Time of main spawning in different areas, 1971.

Table 6. Maturing of capelin (%) in weekly samples from northern Norway during the spawning season 1971.

Date	West of Nordkyn				East of Nordkyn			
	Maturing	Spawning	Spent	Number in samples	Maturing	Spawning	Spent	Number in samples
17 — 23 January	100.0	—	—	97	—	—	—	—
24 — 30 January	100.0	—	—	248	100.0	—	—	119
31 Jan. — 6 February	100.0	—	—	125	100.0	—	—	146
7 — 13 February	100.0	—	—	123	100.0	—	—	273
14 — 20 February	100.0	—	—	119	100.0	—	—	195
21 — 27 February	100.0	—	—	245	100.0	—	—	110
28 Febr. — 6 March	99.0	1.0	—	103	100.0	—	—	131
7 — 13 March	—	—	—	—	100.0	—	—	99
14 — 20 March	32.9	32.9	34.2	365	—	—	—	—
21 — 27 March	—	27.8	72.2	36	57.5	42.0	0.5	200
28 March — 3 April	2.8	45.8	51.4	216	—	—	—	—
4 — 10 April	—	—	—	—	42.9	30.0	27.1	140

in Nordvågen. If it is presumed that males and females were present in equal numbers, this implies that approximately 5000 tons of capelin had spawned.

From the grab samples, the developmental stages of eggs were designated, by comparison with artificially fertilized eggs kept in the laboratory. Thus, approximate dates of spawning were found for the different areas (Fig. 14). At Arnøy, Loppa, Silda, Ingøy and Tarhalsen spawning probably took place between the 15 and 25 March. Spawning at Nordvågen occurred between the 20 and 30 March. At Porsangneset and in the Berlevåg areas spawning most likely occurred about 1 April, in Omgang and Båtsfjord areas one week later. At Loppa and in Nordvågen a new spawning occurred in the middle of April, but in Nordvågen this spawning was of little significance compared to the first one. These spawning times are in accordance with the development of the gonad condition of the capelin (Table 6).

The exact temperature at the time of spawning is not known. In Nordvågen temperature at the bottom was measured on 30 March and 14 April, and was then 1.5° and 3.0° C respectively. An other spawning grounds which were visited two or three weeks after spawning, the temperature varied between 2° and 3°C.

Spawning in 1972 was studied by Bjørke, Gjøsæter and Sætre (1972). Both spawning area and spawning time differed from the conditions in 1971. Spawning depth also showed some difference, especially in the western part of the area. In 1972 the most extensive spawning took place off East Finnmark. Farther to the west, spawning was observed at Magerøy, Hjelmøy, Tarhalsen and Malangsgrunnen—Fugløybanken. At all these localities the spawning depth was greater and the temperature considerably higher than in 1971. At Malangsgrunnen spawning took place at about a 150 m where the temperature was about 6°C. Spawning in 1972 started about 1 March and lasted until the end of March.

In the eastern part of the spawning area, spawning was later than in the western part.

FERTILIZATION AND SURVIVAL OF EGGS

On the spawning beds the fertilization seemed to be almost 100 per cent, while fertilization rates down to about 50 per cent were sometimes observed among eggs brought up by grab or divers. Between 2.5 and 5.0 per cent were mechanically destroyed. It is not known whether this was a result of the sampling or a natural phenomenon. Apart from this, mortality seemed to be very low. Generally, greater mortality was observed where only a few eggs were found than on the proper spawning

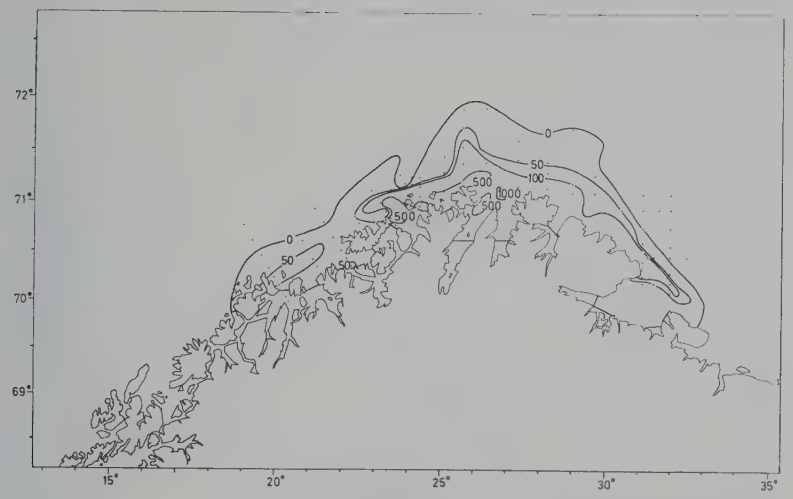

Fig. 15. Distribution of capelin larvae 1—15 May 1971. Isolines indicate the number of larvae below 1 square m surface. Stations are plotted as dots.

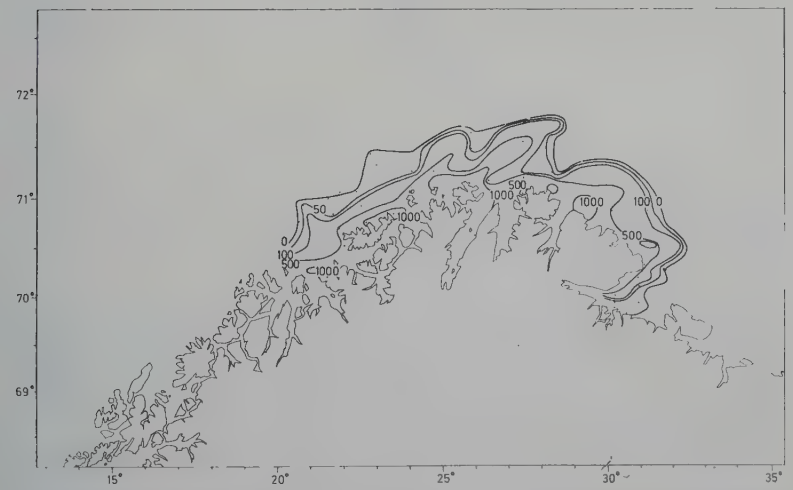

Fig. 16. Distribution of capelin larvae 19—25 May 1971. Isolines indicate the number of larvae below 1 square m surface. Stations are plotted as dots.

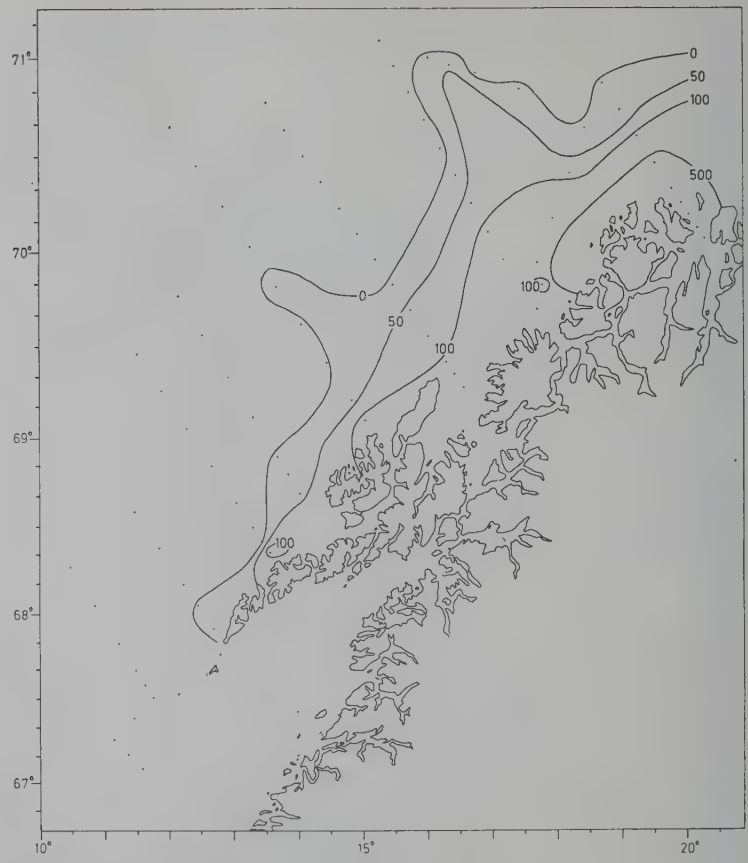

Fig. 17. Distribution of capelin larvae 20—28 May 1971. Isolines indicate the number of larvae below 1 square m surface. Stations are plotted as dots.

beds. An exception was observed at Loppa, where mortalities up to 19 per cent were found in samples with very dense concentrations of eggs. On some of the spawning grounds many eggs were overgrown with small filamentous algae, but this did not seem to cause any retardation of the development or any increase in the mortality rate.

Eggs, together with bottom sediment, were found in the stomachs of capelin and haddock. At the spawning beds investigated, few haddocks were present. Therefore the predation on eggs was not very

intensive and had no serious effect. In 1972 an extensively larger predation by haddock was observed, but only at spawning grounds deeper than 150 m (Bjørke, Gjøsæter og Sætre 1972). According to Zenkevitch (1963) capelin eggs form an important part of the haddock's diet.

Predation on eggs by ducks (*Somateria spectabilis, S. mollissima* and *Clangula hyemalis*) was observed at shallow spawning grounds (Gjøsæter, Sætre og Bjørke 1972), but the quantities consumed are probably of little significance.

Eggs from the upper bottom strata showed a faster development than those laying deeper in the substratum. No difference in mortality was observed at the egg stage, but preliminary results indicate a higher hatching success among eggs from the upper strata.

To evaluate the effects of using fishing gears on the spawning beds, trawl bobbins were towed through one of them (Bjørke and Bakke 1973). No increase in mechanical destruction could be observed, but eggs whirled up from the bottom showed mortalities between 6.0 and 10.2 per cent after being kept in glass jars in the laboratory, while eggs taken from the bottom of untouched spawning beds showed mortalities between 0 and 2.1 per cent when kept in a similar way. This experiment was carried out when the eggs had finished about 2/3 of the developmental time.Studies of eggs in the laboratory suggest that susceptibility to mortality is higher in earlier stages of development and possibly also in the latest. These results, therefore, might not be representative for eggs in other stages.

LARVAL DISTRIBUTION

Five larval surveys were carried out during 1 May to 22 June 1971. The distribution of larvae in each survey is shown in Fig. 15—19. In the first surveys the larvae were distributed close to the shore. During the surveys in June smaller quantities of larvae had drifted from land. Near the shore both newly hatched and older larvae were found, while offshore only older larvae were found. This indicates that spawning in 1971 only occurred in the near shore area.

During the first surveys highest larval concentrations were observed off Troms and West Finnmark, while the latest surveys showed highest concentrations at the coast of eastern Finnmark. This is due to later spawning and lower temperatures in the eastern area.

Number of larvae was determined for each survey by means of an area integration. The following results were obtained:

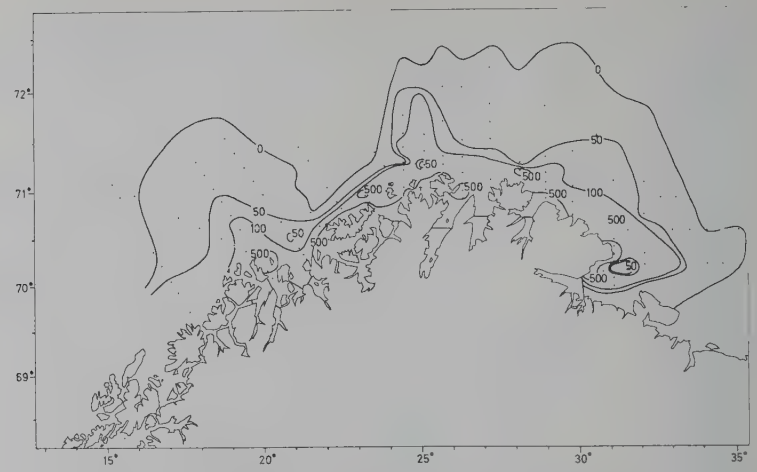

Fig. 18. Distribution of capelin larvae 2—17 June 1971. Isolines indicate the number of larvae below 1 square m surface. Stations are plotted as dots.

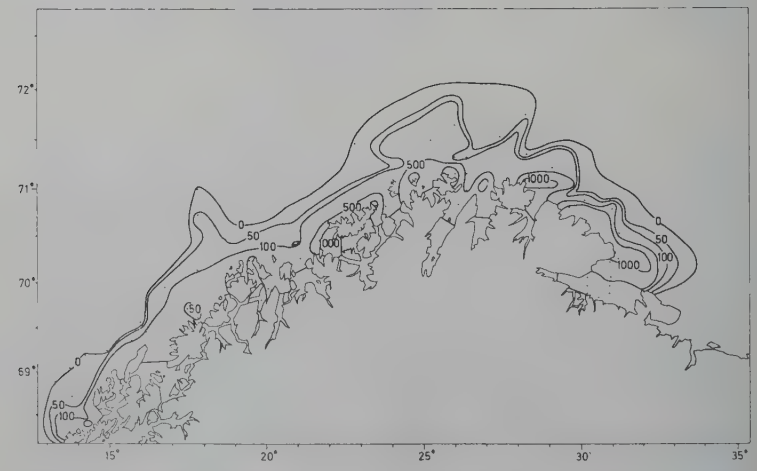

Fig. 19. Distribution of capelin larvae 7—22 June 1971. Isolines indicate the number of larvae below 1 square m surface. Stations are plotted as dots.

1—15 May: $2.8 \cdot 10^{12}$
19—25 May: $1.4 \cdot 10^{13}$
2—17 June: $1.5 \cdot 10^{13}$
7—22 June: $1.6 \cdot 10^{13}$

Although the larval material for 1972 is not completed, preliminary results seem to indicate a more eastern distribution than in 1971.

0- AND I-GROUP ABUNDANCE

During the larval and postlarval stages a drift migration takes place into the central part of the Barents Sea. The younger capelin (0- and I-group fish) are distributed farther south than the two and three year olds. The nursery area of the capelin is extensive, but the main grounds are in the central and eastern part of the Barents Sea. The abundance indices of 0-group fish, obtained from acoustic surveys, give a fairly good estimate of year-class strength (Dragesund 1971).

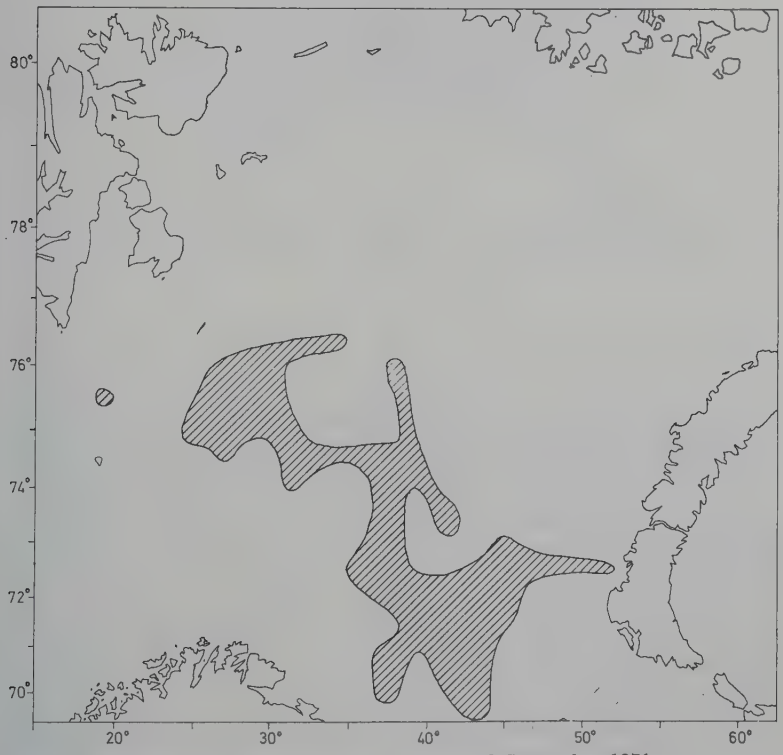

Fig. 20. Distribution of I-group capelin 23 August—9 September 1971.

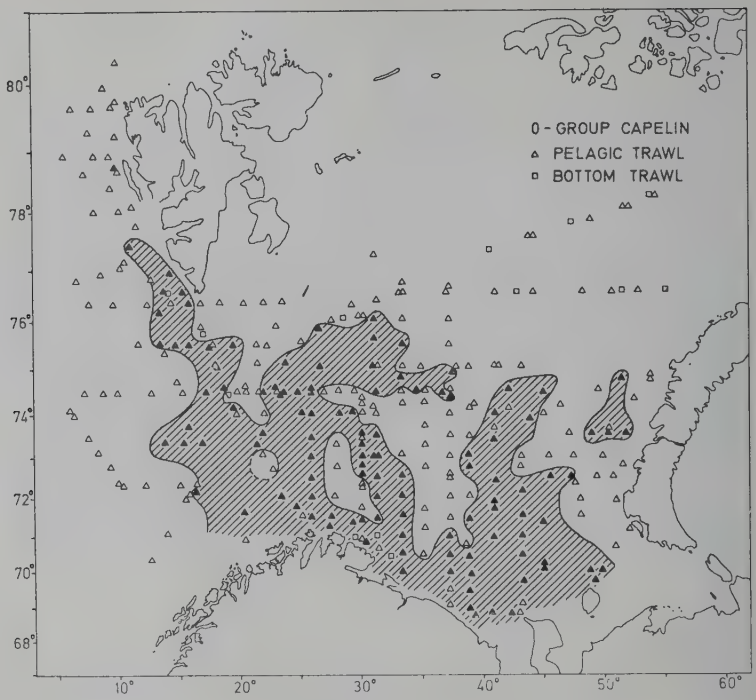

Fig. 21. Distribution of 0-group capelin 23 August—9 September 1971.

In 1970, 0-group capelin were limited to a small area, mainly along the Finnmark and Murman coast and in the eastern Barents Sea (Anon. 1970). The concentrations were rather low, indicating a week 1970 year-class. However, later investigations showed that the I-group capelin were distributed over a fairly wide area (Fig. 20), and, although the 1970 year-class is relatively weak, it is suggested that the year-class is somewhat stronger than indicated from the 0-group survey. In 1971 the abundance of 0-group capelin was not so high as that observed in the years 1967 and 1969 (Benko *et al.* 1970), but was considerably higher than in 1970 (Fig. 21), and the indication is that the 1971 year-class is abundant. The 1972 year-class also seem to be strong (Fig. 22), probably of the same order as that of 1971.

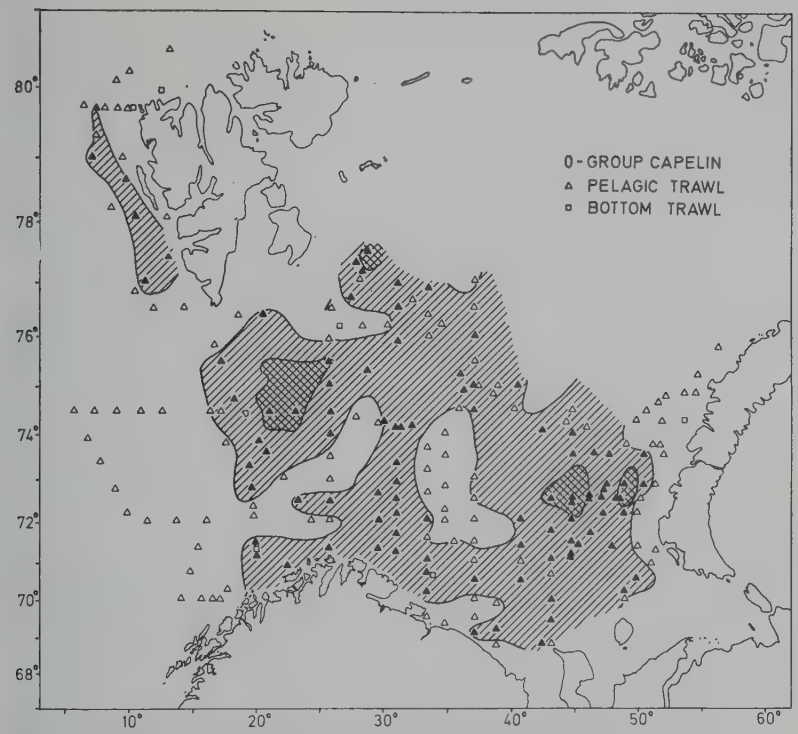

Fig. 22. Distribution of 0-group capelin 27 August—11 September 1972.

DISCUSSION

The availability of capelin was good during the winter seasons 1970—1972. Capelin were distributed over wide areas, the seasons lasted relatively long, and the weather conditions were good. A relatively small part of the stock reached the Murman coast for spawning (Seliverstov, verbal information), and most of the capelin spawned in Norwegian territorial waters in 1971 and 1972.

Table 7. Summary of results of stock size estimates (mill. tons) in 1971 and 1972.

Year	Method		
	Tagging experiments	Egg and larval surveys	Acoustic surveys
1971	5.8	3.2	—
1972	4.8	—	2-3.6

The steady increase in the total catch of capelin since 1965 is due to a significantly increased fishing effort (Bakken and Dragesund 1971), but is also for a large part attributed to a raise in stock size. Some indication of the relative variation in the size of the spawning stock in 1969—1972 might be obtained from year-class strength estimates at the 0-group stage (Anon. 1969, Benko *et al.* 1970).

These estimates indicated that the 1966, 1967 and 1968 year-classes exceeded the year-class of 1965. The ranking of the 1966, 1967 and 1968 year-classes were difficult to assess from the 0-group fish surveys. However, later information from catch statistics and echo surveys, suggests that the 1967 year-class was significantly stronger than those of 1966 and 1968. Since four year old fish predominated in the spawning stocks in 1969—1972, it is likely that the spawning stock was higher in 1970 than in 1969, and again the stock strength was greater in 1971 than in 1970 and 1972.

Although the stock size estimates for 1971 and 1972 must be interpreted with caution, they indicate that the spawning stock in 1971 was greater than in 1972 (Table 7).

With the fragmentary knowledge of stock size and of the relationship between stock size and reproduction of capelin, it is difficult to state that the exploitation rate is too high. A study of capelin reproduction during the period 1951 to 1961 indicated, however, that although the stock size probably was much lower than now, there were no clear correlation between parent stock size and subsequent recruitment (Gjøsæter 1972). This, and the investigations carried out during the last two years, indicate that no immidiate further steps are needed to secure a high spawning potential. On the other hand, it is possible that the intensive fishing during the prespawning and spawning period may have unfortunate influence on spawning behaviour.

The spawning stock was at a very high level in 1971 and fairly high in 1972. The resulting year-classes measured at the 0-group stage seemed to be abundant. The 1969 year-class is also estimated to be strong (Anon. 1969). The relatively low production in 1970 was most likely due to environmental factors and not to small spawning stock, and so far no sign of overfishing has been observed.

ACKNOWLEDGMENTS

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Mrs. Iversen has also assisted, and Mrs. Fylkesnes has corrected the English text.

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DIVING OBSERVATIONS ON BARENTS SEA CAPELIN AT THE SPAWNING GROUNDS OFF NORTHERN NORWAY

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ABSTRACT

Bakke, S. and Bjørke, H. 1973, Diving observations on Barents Sea capelin at the spawning grounds off northern Norway. *FiskDir. Skr. Ser. HavUnders.*, *16*: 140—147.

During the spring of 1971 divers made observations at the spawning grounds of the Barents Sea capelin.

Large masses of capelin eggs were found at two localities: Loppa, (35—70 m depth) and Nordvågen (12—18 m depth). The eggs were mixed down to a depth of 5 cm with fine gravel (0.5—1.5 cm diameter).

Two behaviour patterns of the capelin were observed: Loosely packed schools in the upper layers and dense circulating schools close to the bottom. The latter are believed to be males waiting for ripe females.

Egg mortality caused by trawlers was experimentally investigated by dragging trawl bobbins along the egg beds. Eggs stirred up by the bobbins showed higher mortality (up to 10.2% after ten days incubation) than undisturbed eggs and eggs from bobbin tracks (up to 2.5% mortality after ten days incubation). Less than 1% of the eggs on the investigated spawning grounds is believed to be damaged by trawlers.

Diverse estimated a 5—10% decrease in the number of eggs on the spawning grounds over a four week period. This was due to a drift of eggs largely caused by wave action and water currents.

No predation of the capelin eggs was observed.

INTRODUCTION

The aim of this investigation was to obtain information about the spawning grounds of the Barents Sea capelin, the fishes' behaviour and the egg mortality on these grounds. The observations were made in spring 1971.

The spawning behaviour and the morphology of the spawning grounds have been described for the Newfoundland capelin. Templeman (1968) reports both beach spawning and spawning down to at least 55 m. A substrate of fine gravel from 0.25 to 1.50 cm in diameter seemed to be especially favourable for capelin spawning (Templeman 1948). On the offshore spawning grounds the bottom substrate was somewhat finer, from 0.5 to 2.2 mm in diameter (Pitt 1958).

Spawning behaviour and spawning grounds of the capelin in the northeastern Atlantic have not been well investigated. Collett (1903) reports that the capelin search along the shores of bays and fjords for suitable spawning grounds. He mentions that spawning mostly takes place on sandy bottoms, sometimes at depths of only a few metres, but

more often at depths of 70 to 90 m. Prokhorov (1965) refers to Russian authors who unanimously state that spawning takes place on sandy grounds with an admixture of fine shell gravel. He concludes that a depth range of 50 to 100 m at the spawning places is most usual while Møller og Olsen (1962) suggest that spawning takes place at depths of 10 to 100 m.

MATERIAL AND METHODS

Capelin were found all along the coast of Finmark by using echo sounders. Schools were also observed by divers at three different localities: Hasvik, Trollsund and Nordvågen. (Fig.1) Photographs and films were taken of the fish as close as 0.4 m.

The diving was carried out from the R.V. «Johan Hjort» during the period 15 March — 29 April 1971. The sampling gear included a stainless steel box designed by the authors to take 0.1 m² samples from sand and gravel bottoms and two frames of 1.0m² and 0.1m² for sampling algae and stones from specific areas. At least two bottom samples were taken at each diving locality. Temperatures were measured on the bottom and in the sediment, and the speed and direction of the current was determined. The diving equipment used is described by Bakke and Bjørke (1971).

Grab samples were also taken at various localities along the coast to check for the presence of eggs. A total of 46 dives were made.

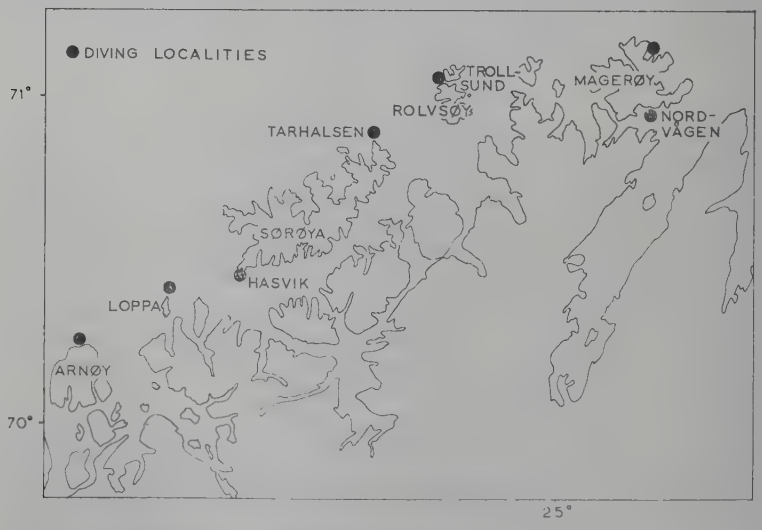

Fig. 1. Diving localities in the investigated area.

RESULTS

OBSERVATION ON CAPELIN SCHOOLS

Two different behaviour patterns of the schools could be distinguished. Firstly, and most commonly, the schools could be at least 100 m in length and 20 m in width and depth. The fish swam slowly, well above the bottom at depths between 5 and 20 m and were about 40 to 80 cm apart. Initially they reacted simultaneously to movement by the divers, but this reaction eventually ceased as they became accustomed to the divers' presence. The schools changed course several times while observed; they often made a wide circular movement, but whether this was due to the presence of the diver or not, is unknown.

Secondly, the schools swam close to the bottom (20 m) in a very dense formation with the fish less than 10 cm apart. The schools were sharply delineated in all directions and were less than 2 m in depth. The school was most dense nearest the bottom with the fish head to tail and their sides nearly touching. The movement of the school was still circular, but within a very small radius. These schools did not react to the presence of the divers and pictures could be taken from as near as 0.4 m with the school in effect circulating around the divers. The pictures indicate that such schools consisted mainly of males (Fig. 2).

Individuals were frequently seen to lag behind the schools. Such

Fig. 2. Male capelin circulating around the photographer at Nordvågen.

fish were found either close to the bottom or near the surface; sometimes they even swam upside down. These individuals did not show any external signs of abnormality other than the often bloodshot and swollen base of the male anal fin.

At Nordvågen (Fig. 1) where extensive trawling took place, large masses of dead capelin were seen on the bottom. Whether this high mortality was the result of spawning or fishing by trawlers, is not known. Dead fish were seen at all diving localities, but it must be concluded that the dead capelin seen at Hasvik died a natural death as no fishing had taken place there. All samples of dead fish consisted of spent males.

OBSERVATIONS AT THE SPAWNING GROUNDS

At Loppa and Nordvågen (Fig. 1), where the greatest egg masses were found, the substrate changed progressively with increasing depth, starting with rocks and boulders just below the surface and ending with fine sand. This sequence did not occur at the other six localities where only small numbers of eggs were found attached to algae and stones.

The main spawning ground at Loppa was much more exposed to wave action than the ground at Nordvågen. The shallowest edge of the spawning bed at Loppa was at 35 m where coarse gravel was succeded by finer gravel with a grain size of 0.5—1.5 cm. Grab samples revealed that the gravel and egg mixture extended to at least 70 m water depth. The concentration of eggs on this ground was the highest observed; and numerous clumps consisting only of eggs were seen.

The other more closely observed spawning locality was just outside Nordvågen (Fig. 3). This relatively sheltered area had fine gravel from 12 to 18 m in depth with coarse gravel at lesser and sand at greater depths. Divers surveyed the main spawning ground and found it to be about 180 000 m^2. No eggs were found closer than 250 m to the shore. The ground consisted of fine black gravel and was bordered either by coarser gravel with stones or by sand (Fig. 3). Grab samples which covered a greater area, later confirmed these observations and showed that the main spawning ground lay within the area of the fine gravel (Dragesund, Gjøsæter and Monstad 1971). Eggs were found in the substrate to a depth of about 4 cm in the centre of the main spawning ground, but penetrated less deeply towards the borders. Samples from the centre indicated a density of about 3×10^6 eggs per square m. On one occasion, a diver's sample taken from fine sand at greater depths showed densities of up to 4×10^5 about 100 m from the main spawning ground.

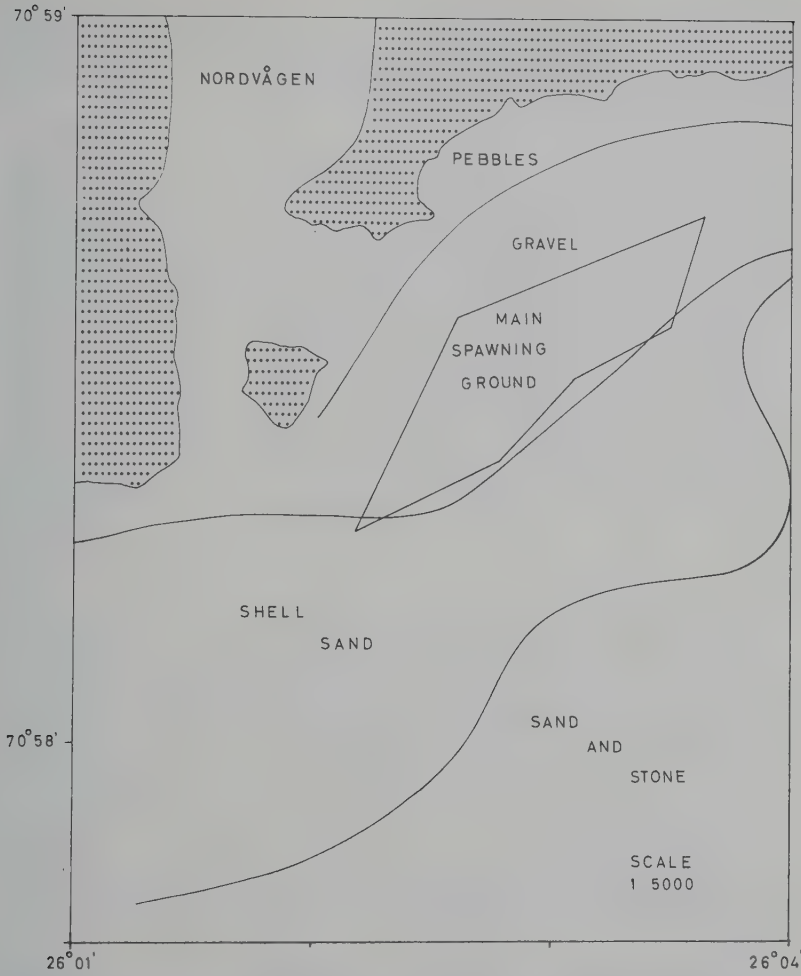

Fig. 3. The spawning ground at Nordvågen. The lines separate different bottom substrata.

The ground at Nordvågen was examined three times, from 29 to 31 March, from 14 to 16 April and on 25 April. During this time the sea temperature near the bottom rose from 1.5°C to 3.2°C. During dives on 14 April the temperature was measured at intervals of 40 m across the spawning area just above the egg layer and at about 5 cm down into the substrate. The water temperature ranged from 3.2°C offshore to

2.8°C nearest the shore. The bottom substrate was consistently slightly cooler than the water above. The current direction at 5 m above the bottom, measured over a 29 hour period, was mainly northnortheast, and the current speed varied from 13 to 46 cm per sec.

From 14 to 16 April and on 25 April, brown patches caused by a filamentous algae that settled on both the stones and the eggs, were observed on the beds. They seemed to have no effect on the eggs since samples of eggs with algae kept in jars did not show a higher mortality than eggs without attached algae (Dragesund, Gjøsæter and Monstad 1971). Only a few laminarians and starfishes were found at the spawning ground, and capelin were the only fish observed.

Between 29 March and 25 April a marked decrease was noted in the number of eggs on the surface of the substrate. Below the surface, however, the concentration of eggs remained high during the entire investigation. Drifting eggs were observed at both the Nordvågen and the Loppa grounds except during calm weather. The total decrease in eggs at Nordvågen was probably between 1×10^5 and 4×10^5 eggs per square m.

DAMAGE TO CAPELIN EGGS BY TRAWLERS

Norwegian fishermen have suggested that the lower doors of pelagic trawls may damage capelin eggs if dragged along the spawning beds. Tracks made by trawl doors were observed at the spawning grounds in Nordvågen. These drag marks were about 0.5 m wide and usually more than 40 m long with ridges of an egg and gravel mixture about 10 cm high on one side of the tracks. Altogether, such tracks covered less than 1% of the spawning area.

Several samples were taken from the middle of the tracks and from the top and bottom of the ridges. The proportion of damaged eggs (2.5—5.0%) in these samples was similar to that in samples taken outside the tracks.

An experiment was carried out in Nordvågen to study the effects of mechanical disturbance of the eggs. Three trawl bobbins were hauled along the spawning beds while a diver observed the effect. The bobbins stirred up the eggs and bottom substrate and made tracks on the bottom similar to those made by trawl doors. Egg samples were taken from the tracks and from an undisturbed area nearby, while a plankton net, placed behind and above the bobbins, sampled the eggs which were stirred up. There was no difference in the proportion of damaged eggs, or their subsequent mortality, between the samples taken from the tracks and those from undisturbed areas. Whereas the mortality of

both these types of samples, kept for 12 days in glass jars, was between 0 and 2.1% (Dragesund, Gjøsæter and Monstad 1971), the mortality of eggs caught in the plankton net ranged between 6.0 and 10.2%.

DISCUSSION AND CONCLUSIONS

The behaviour patterns observed on the spawning grounds in northern Norway resemble observations made by Sleggs (1933) in Canada where the schools of mature capelin formed either a dense globular mass or an elongated streak of swimming fish. Templeman's statement (1948) also supported this when he described capelin schools prior to spawning and observed that these schools, as in the case of the Barents Sea capelin, consisted entirely of males. In addition, he stated that male capelin are mature when they approach the shore for spawning, and that they are in constant attendance at the beaches. Schools of immature females stay in shallow water, away from the immediate neighbourhood of the beach, and as they reach maturity, swim in groups to the beach to spawn.

The indication in the present results, that greater numbers of eggs are found where there is fine gravel, agrees with observations from the main spawning grounds in Canada (Templeman 1948). Only once, at Nordvågen, were large number of eggs found in fine sand close to the main spawning ground. Although sand seems to be a less suitable substrate, it is possible that mass spawning can occur there when the best ground is occupied or when the spawning pressure is great (Templemann 1948).

Templeman (1948) and Sleggs (1933) found that spawning movements could bury the eggs to some extent, but most of the burying, to a depth of one foot, was the result of wave action. This did not seem to be the case on the spawning grounds observed in this investigation, since the depth of 35 to 70 m at Loppa and the sheltered conditions in Nordvågen probably prevented strong wave action. It was noticed, however, that the egg and gravel mixture could be stirred up by slight water movements made by the diver's hand just above it due to the extra buoyancy of the gravel with eggs stuck to it. Thus, eggs can be buried more easily when repeated spawning occurs on the same ground. When the egg and gravel mixture reached a maximum thickness of 5 cm, as at Loppa, clumps of eggs were formed after additional spawning.

Dragesund, Gjøsæter and Monstad (1971) reported that both the natural egg mortality of the spawning grounds and the mortality of the disturbed eggs was low. However, Burd and Wallace (1968) carried out laboratory experiments on mechanically disturbed herring eggs and

found that trawling at the spawning grounds might induce a reduction in larval viability. During the investigation, intensive trawling at or near the Nordvågen spawning ground yielded 7300 tons of capelin. In spite of this, less than 1% of the spawning ground was disturbed by the trawl doors. Even if all the disturbed eggs did die, this would affect less than 1% of the eggs at Nordvågen. Pelagic trawling at the spawning grounds therefore seems to have little influence on overall egg mortality.

At Nordvågen, a decrease of 5 to 10% in egg numbers due to drift was observed over a four week period. Since a similar drift of eggs was also observed at Loppa, this may well be the greatest source of loss there and in other areas.

ACKNOWLEDGEMENT

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AN INTRODUCTION TO A STUDY OF THE MARINE ECOSYSTEM AND THE LOCAL HERRING STOCK IN LINDÅSPOLLENE

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ABSTRACT

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A study of the marine ecosystem in a landlocked fjord (Lindåspollene) with a self-contained herring stock has been initiated. On the basis of preliminary investigation a brief description of topography, hydrography and general biological features of the Lindåspollene is given. The plans for the projected long term research are described and discussed.

INTRODUCTION

At the 1961 symposium on «Herring population studies», arranged by the International council for the exploration of the sea, (ICES), the following recommendation was adopted (Anon. 1969):

> «In view of the size and great complexity of the biological, ecological and other processes governing the population dynamics of the herring stocks, and of the extent and complexity of scientific problems involved in understanding them, the Symposium recognizes the need for setting up intensive and comprehensive studies on a small, self-contained, easily accessible herring population. It further recognizes that such populations are known to exist in at least one member country. It therefore recommends that the Herring Committee of ICES should explore the possibilities of such investigations being initiated».

As a result of this recommendation a special working group was set up to study various localities, particularly within the Norwegian fjord systems which might meet the requirements for these studies.

The working group studied three localities near Bergen: Heiamarkpollen 36 km south of Bergen, Fjellspollen 18 km southwest of Bergen and Lindåspollene 36 km north of Bergen (Anon. 1969). The only really

self-contained stock was found in Lindåspollene, but the working group agreed that the herring in Fjellspollen was of greater interest as it contained both spring and autumn spawning populations.

For various reasons the ICES did not find it possible to embark on the proposed research programme, but recommended that national laboratories started such investigations either individually or on a bilateral basis.

The Institute of Marine Research, Directorate of Fisheries, decided to follow up the Council's recommendations on a national basis. Lindåspollene were selected for the study because the herring stock there is largely self-contained and only slightly influenced by herring stocks in the surrounding fjord sytsem (Anon. 1969). As important parameters of the herring population are intimately related to chemical, physical and biological conditions in the environment, it was felt that a comprehensive study of the entire ecosystem would be desireable. In order to undertake such a study it was necessary to engage other marine laboratories, and in 1970 a cooperative research programme for the study of herring and its environment in Lindåspollene was initiated with the Biological station, Espegrend, University of Bergen.

In 1971 a large industrial complex was planned at Mongstad, which is located about 15 km north of Lindåspollene. In connection with this development a housing project for about 200 persons is under construction near Lindås (Fig. 1), and for a period of four years sewage from these houses will be discharged into Lindåspollene. As further urbanization of the area must be expected, a study of the effect of sewage pollution on the dynamics of the ecosystem will be one of the important aspects of the investigation.

The purpose of the present paper is to give a preliminary description of the environmental and biological features of the Lindåspollene ecosystem, and to present the objectives and long term plans for the investigations.

GENERAL DESCRIPTION OF LINDÅSPOLLENE

TOPOGRAPHY

Lindåspollene consist of three major basins separated by shallow sills (Fig. 1). The outermost basin, Straumsosen, with adjacent inlets has a surface area of 2.205×10^6 m^2, and it has access to the Lurefjord through three narrow channels. The maximum depth in Straumsosen is about 60 m, and the sill depth between Straumsosen and the middle basin, Spjeldnesosen, is 5—10 m. Spjeldnesosen is the deepest and largest of the basins with a surface area of 3.782×10^6 m^2 and a maximum

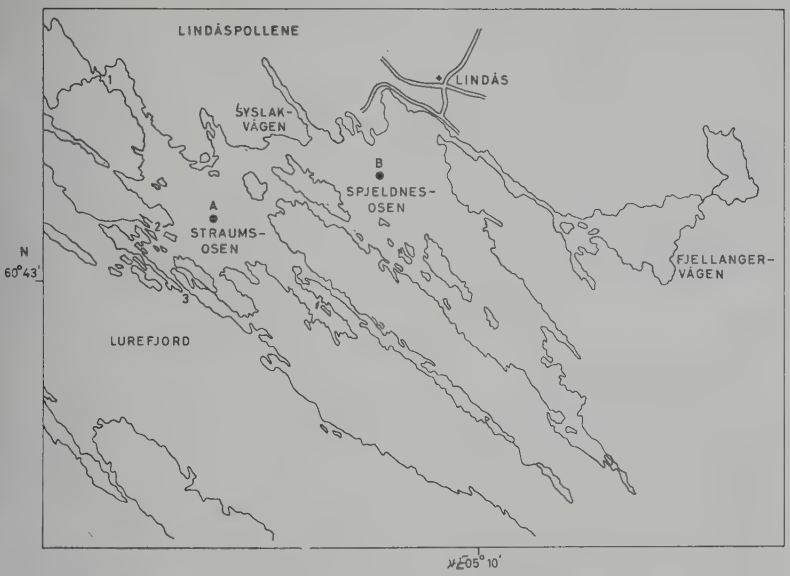

Fig. 1. Lindåspollene. A and B) Hydrographical stations, 1, 2 and 3) outlets to Lurefjord.

depth of about 90 m. A narrow channel about 2 km long leads into Fjellangervågen, the smallest of the three basins, with a surface area of 0.885 $\times$ 10^6 m^2 and a maximum depth of about 80 m.

The shores around Lindåspollene are generally rocky and steep, but at the heads of the inlets there are beaches with bottom types ranging from gravel to soft mud. The sediments of the bottom deeper than about 25 m in the major parts of Fjellangervågen and Spjeldnesosen consist of a very soft, black ooze whereas in Straumsosen they consist of a mixture of mud, sand, gravel and shell-fragments.

The landscape surrounding Straumsosen is rocky and barren which is characteristic of the outer West-Norwegian coastline. Fjellangervågen and the southern half of Spjeldnesosen are surrounded by farmland and pine forest. In general the area is sparsely populated, and there is very little industry. The district of Lindås (Fig. 1) has a population of about 300, and about the same number of people inhabit the farms in the surrounding area.

HYDROGRAPHY

The tidal range measured on 8—9 December 1970 was 35 cm, but according to local residents the average range is about 50 cm. With a total surface area of 6.872 $\times$ 10^6 m^2 and a total volume of 153.313 $\times$

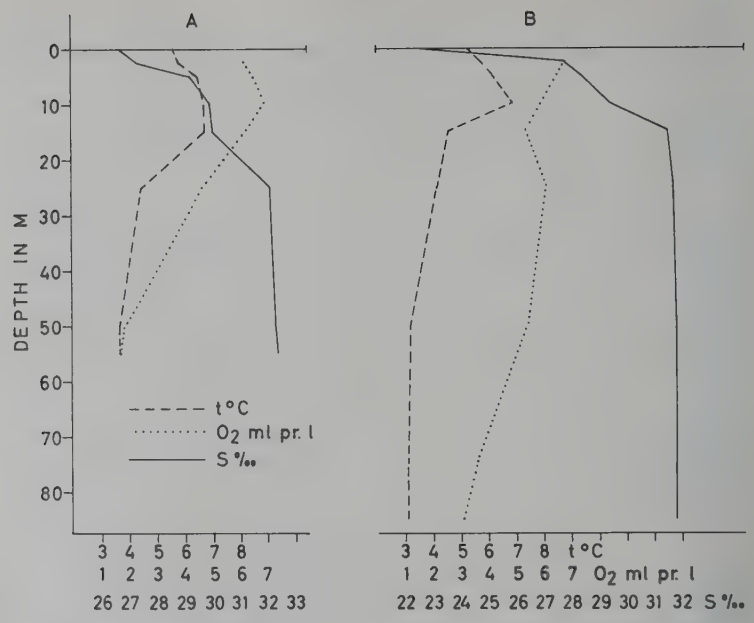

Fig. 2. Vertical distribution of temperature, salinity and oxygen at station A in Straumsosen and station B in Spjeldnesosen, 8 December 1970.

10^6 m^3 the exchange of water during a tidal cycle would be about 3.436×10^6 m^3 or about 2% of the total volume.

Fjellangervågen, the southern half of Spjeldnesosen and the inlets adjacent to Straumsosen are as a rule covered by ice about 2—3 months each winter.

A small lock used to be in operation in one of the entrances to Lindåspollene (2 in Fig. 1), but because of a decline in shipping in the area the lock gates have been permanently open since 1964. According to local residents this has had a marked effect on the water masses in Lindåspollene as evidenced by a distinct reduction in ice cover. An additional effect may be increased immigration and emigration of fish.

Preliminary investigations carried out during 1964 showed that Fjellangervågen differed from the rest of Lindåspollene in having hydrogen sulphide in the water at depths in excess of about 25 m. Partly for this reason and partly because of the long ice cover in the area, Fjellangervågen will not be studied during the first part of the investigations in Lindåspollene.

Fig. 2 shows the vertical distribution of three hydrographic para-

meters in the centre of Straumsosen (A) and Spjeldnesosen (B) on 8 December 1970. The watermasses below 25 m in Straumsosen and below 15 m in Spjeldnesosen were rather homogeneous in salinity and temperature, whereas the oxygen values showed a sharp decline with depth in Straumsosen. The surface salinity was considerably lower in Spjeldnesosen than in Straumsosen, and in the deeper layers the salinity at the former station was about $0.5^0/_{00}$ lower than at corresponding depths in Straumsosen. The temperatures of the watermasses deeper than about 25 m ranged from 3.1 to 4.5°C, which is 2—3°C lower than the bottom temperatures of West-Norwegian fjords (Aasen 1952, Sælen 1962).

GENERAL BIOLOGICAL FEATURES IN LINDÅSPOLLENE

The benthic macrovegetation in the area is sparse and largely limited to Straumsosen and the northern part of Spjeldnesosen. Large parts of the shore are too steep for macrovegetation to be successful, but where it is a convenient slope there is some growth of *Ascophyllum nodosum, Fucus vesiculosus* and *F. serratus*. At depths of 5—8 m dense concentrations of calcareous algae, (*Lithothamnium fornicatum*), have been observed, and at depths of 1—3 m some *Laminaria saccarina* also occurs (Svendsen, verbal information). On bottoms of sandy mud at the head of the inlets are small concentrations of eel-grass (*Zostera marina*).

The zooplankton studied during December 1970 revealed a very low species diversity, but an extreme dominance of *Pseudocalanus elongatus* in the uppermost 50 m. In the deeper layers of Spjeldnesosen the zooplankton was dominated by copepodite stage V of *Calanus finmarchicus*. Other abundant forms were *Oithona* spp., *Oncaea* spp., and small chaetognaths. The zooplankton biomass measured as displacement volume was about 0.1 ml/m³ in the 0—25 m layer, about 0.2 ml/m³ in the 25—50 m layer, and in the deepest parts of Spjeldnesosen (50—85 m) it was about 1.0 ml/m³.

Qualitative samples of the benthos collected by an epibenthic dredge with a net of 0.5 mm mesh size revealed significant differances between the two basins. In Spjeldnesosen the net was full of a black, evil smelling ooze, and no animals were found after sieving with 1.0 mm mesh size. In Straumsosen the dredge contained a mixture of mud and sand with only a faint smell of hydrogen sulphide. The fauna was dominated by the cumacean *Diastylis rathkei,* the polychaetes *Chone duneri,* species of the family Aphroditidae and the brittle-stars *Ophiura albida, O. affinis,* and *O. sarsi*. A few specimens of the cumacean *Leucon nasicus* and the mysid *Mysis mixta* also occurred in the samples. The latter species has not previously been recorded south of Trondheimsfjorden.

Observations made by SCUBA-divers supported the impression of a low species diversity in the area (Samuelsen and Høisæter, verbal information). The muddy bottoms deeper than about 30 m in Spjeldnesosen were dominated by the polychaete *Chone duneri,* and the rocky bottoms at depths between 20 and 30 m by sedentary polychaetes, particularly *Placotegus tridentatus.* In the latter zone large individuals of the Iceland scallop, *Chlamys islandica* were observed.

In Straumsosen the fauna appeared more diverse, but largely the same species dominated as in similar habitats in Spjeldnesosen. *Chlamys islandica,* however, did not occur in Straumsosen. The tunicate *Ciona intestinalis* was very abundant at depths from 3 to 15 m and completely dominated the benthos on hard bottoms. This species was also observed along the rocky shores of Spjeldnesosen.

In Straumsosen an individual of the mysid *Heteromysis formosa* was found. Only one specimen of this species has previously been recorded in Norwegian waters (Brattegard, verbal information).

Oysters (*Ostrea edulis*) were previously grown commercially in inlets adjacent to Straumsosen, but the oyster industry tapered off during the years following World War II and is presently nonexistent (Solheim, verbal information).

Herring has been caught commercially in Lindåspollene for centuries and sold locally or on the Bergen fish market. Gill nets were the traditional gear, but beach seines and in recent years purse seines have also been used. Estimates of the fishing effort and annual catch are only available for recent years. Gill nets are used by local inhabitants particularly during the spawning season, and during August—September a few small purse seiners using artificial light have operated in the area. The estimated gill net catch is less than five tons per year, and the purse seine fishery yielded about 15 tons. Assuming 20 tons as the maximum sustainable yield and five years as the turn-over time (Fig. 3), the minimum standing stock would be about 100 tons. This stock size would satisfy the requirements defined by the ICES working group (Anon. 1969).

Investigations of herring samples taken during 1963—64 showed that the population was a spring spawning one, differing from the oceanic stocks in racial characters such as vertebral counts and growth rate. The mean length of the herring at the end of the fourth year of life was 24.5 cm. A similar slow growth of herring has been found in other landlocked fjords such as Lusterfjorden (Aasen 1952).

Bimodality in the length distribution (Fig. 3) indicated a small degree of mixing with other stocks (Anon. 1964). The two components in the samples were easily distinguished by growth rate and vertebral counts. The component with relatively slow growth and a low vertebral

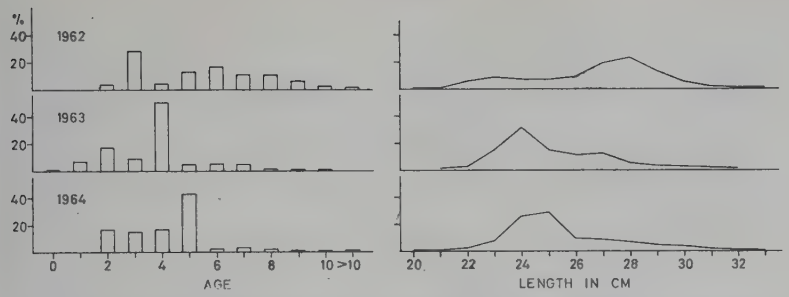

Fig. 3. Age and length distribution of herring from gill net catches in Lindåspollene during 1962—64.

count was overwhelmingly dominant during 1962—64. This group consisted of herring up to 14 years old, but the 1959 year-class was the most abundant. Tagging experiments carried out in November 1962 have shown that some herring migrate out of Lindåspollene, but it is not clear to which component of the population the recaptured fish belonged.

According to information received from the local people, the herring spawn particularly in a small area of Syslakvågen at depths from 0—5 m. In some years scattered spawning has also occurred in other areas near Syslakvågen.

The period of spawning is in the second half of March. The maturity stage distribution in samples collected during 1962—64 confirm that March is the main spawning period, but occasional individuals in spawning condition were recorded until early May.

In autumn the purse seiners also catch sprat (*Clupea sprattus*) together with herring in Straumsosen. There are no reports of spawning sprat from Lindåspollene, and they are most likely immigrants from the outside fjord system.

Other fish species such as mackerel (*Scomber scombrus*), cod (*Gadus morhua*) and pollock (*Pollachius pollachius*) are caught by local fishermen, but none of these species is sufficiently abundant to be of any commercial value.

Species of Cottidae, Labridae and Gobiidae occur along the shores everywhere in Lindåspollene. The Gobiidae particularly are sufficiently abundant to play a significant role in the energy budget of the ecosystem.

PROJECTED LONG TERM RESEARCH

THE ECOSYSTEM

The ultimate aim of the ecosystem studies in Lindåspollene is to build a dynamic mathematical model of the energy flow through and

the cycling of matter in the ecosystem. By model simulation and optimization (Watt 1968) it is hoped to gain sufficient insight into the intricacies of the biological situation to be able to manipulate the system for the benefit of man. Optimal management of the system would involve attempts to increase the yield of the herring fishery, to cultivate marine molluscs and crustaceans and to guarantee continued recreational use of the area.

As no information is available at present about either the biotic or the abiotic properties of the ecosystem, it is felt that it is premature to think in terms of a model at an advanced level of sophistication. Rather, the immediate aim is to gather pertinent information on which to build a crude box model of energy transfer in accordance with the concept of trophic levels (Lindeman 1942). The box model will be the basis for further modelling of the entire ecosystem or sub-sets thereof.

In order to understand the observed temporal and spatial variability in biological properties one must be able to monitor the important hydrographic parameters, i.e. the vertical and horizontal movement of the water masses, and the heat and salt budgets. Eventually, attempts will be made to build a mathematical model for the water circulation in Lindåspollene.

The projected immediate (a) and long term (b) research of the Lindåspollene ecosystem is summarized below.

Hydrography

a) Annual cycles in major parameters such as temperature, salinity, density and oxygen in the water column in Straumsosen and Spjeldnesosen.

b) Horizontal and vertical movements of the water masses, the salt budget, the heat budget, mathematical modelling of circulation.

Botany

a) Primary production and standing crop of phytoplankton and benthic diatoms, standing crop of macrovegetation.

b) Modelling of primary production in relation to environmental parameters such as light, nutrients and physical properties of the water masses.

Zooplankton

a) Quantitative composition, diversity, seasonal fluctuations, trophic groupings, standing crop.

b) Energy flow through populations of dominant species, modelling the «interrelationships» between phytoplankton and zooplankton.

Zoobenthos

a) Distribution and species composition of benthic communities, standing crop, trophic groupings.

b) Energy flow through populations of dominant species in the infauna and epifauna, quantitative studies of meiofauna, total oxygen comsumption by the sea bed.

Fishes (other than herring)

a) Energy flow through populations of gobiid fishes, particularly *Gobius flavescens.*

Microbiology

a) Rate of decomposition of organic matter and regeneration of nutrients in the water masses and in the sediments.

Systems analysis

a) Introductory box models of energy transfer, efficiencies between trophic levels.

b) Dynamic modelling, simulation experiments.

The research listed as a) above is presently under way or near completion except for the microbiological aspects. The most efficient way of carrying out large scale ecosystem analyses would be to engage experts in the various disciplines. As neither the funding nor the qualified manpower available permit this, the policy is to engage graduate students in oceanography, fisheries and marine biology in addition to permanent research staff at the Institute of marine research and the Biological station, Espegrend. Projects for the students have been selected with the aim of providing pertinent data for the initial modelling. This approach has the added advantage of training students in team efforts and integrated research.

THE HERRING INVESTIGATIONS

The vertical and horizontal distribution of the herring will be investigated by echo surveying. This programme will be performed by monthly or fortnightly surveys along permanent transects in the area. Particular studies of stock assessment using acoustic methods will be made at selected times of the year when the herring distribution is most suitable for such studies.

Sampling with gill nets of various mesh sizes will be performed monthly, and the material will be analysed in order to monitor the maturation cycle of the stock and to estimate individual growth.

Mesh selection in gill net catches prevents true estimates of the age composition of the stock and therefore some purse seining will be done in summer or autumn. Commercial fishing has shown that during this season the herring is particularly susceptible to purse seining, especially if combined with the use of artificial light.

As the herring in Lindåspollene spawns in shallow water in well defined areas, the stock is particularly suited for studies of spawning behaviour and estimation of the spawning stock. Attempts will be made to estimate the spawning intensity by mapping the spawning area and counting the abundance of eggs per unit area. Variation in spawning time from year to year in relation to chemical and physical properties of the environment will be studied. Hatching time can be estimated by frequent larval surveys on the spawning grounds, and the dispersal and survival of larvae will be investigated in the period following hatching. In this connection it is of particular interest to test the efficiency of various types of sampling gear.

Estimates of the rates of survival of the herring in Lindåspollene can probably only be obtained from tagging experiments. Tagging with Lea's external tags in 1962 resulted in extremely high numbers of returns because the externally tagged fish were highly vulnerable to gill nets. On the other hand, returns from internally tagged fish will be severely underestimated because the herring is used exclusively for human consumption, and such tags are only occasionally observed when the fish are gutted. Recent developments in tagging techniques (Gundersen 1960) combine the advantages of external and internal tagging, and these methods may be suitable for tagging experiments in Lindåspollene. As no regular commercial fishing takes place in the area, the tagging operations will have to be followed up by an extensive fishing effort.

When the various parameters of the herring population have been estimated with reasonable confidence intervals, an attempt will be made to build computer models of the population dynamics which may be amenable to simulation experiments aimed at suggesting refinements of the model.

The herring stock in Lindåspollene is well suited for short term biological and experimental studies as recommended by the ICES Working Group (Anon. 1969). Such studies include behavioural studies, genetical studies, experiments with tagging techniques, and experiments with sonar equipment for estimating fish abundance, target strength etc.

THE POLLUTION STUDIES

A research programme has been started to measure the possible effect of the sewage discharge into Lindåspollene on the production of phytoplankton and on the steady state conditions generally. Primary production measurements by ^{14}C-technique, chlorophyll estimates, and estimates of total organic matter in the water masses will be carried out throughout the year, and physical and chemical parameters such as light, temperatures, salinity, oxygen, nitrates, nitrites, ammonium, silicate, phosphate, and pH will be measured simultaneously.

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AGE DETERMINATION AND THE GROWTH AND AGE DISTRIBUTION FROM CEMENTUM GROWTH LAYERS OF BEARDED SEALS AT SVALBARD

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ABSTRACT

Benjaminsen, T. 1973. Age determination and the growth and age distribution from cementum growth layers of bearded seals at Svalbard. *FiskDir. Skr. Ser. HavUnders.*, *16*: 159—170.

Material for this study was collected from 177 bearded seals on a sealer at Svalbard in 1968 and from 18 seals studied by biologists at Svalbard and in the Barents Sea in 1968 and 1970.

Bearded seal teeth degenerate and are lost at an early age, but canines in the upper jaw remain, apparently throughout life. They wear down at a linear rate. Dentine cannot be used for age determination, but cementum growth layers are added annually and permit age determinations also of adult seals. Growth layers in claws wear off after about 10 years. Bearded seals grow to a mean adult length of 225 cm at about 10 years. Females are slightly, but not significantly, larger than males. At Svalbard age-groups are fully recruited at 9 years and live to an age of about 31 years. A total annual mortality of 0.14 has provisionally been estimated for adult bearded seals at Svalbard.

INTRODUCTION

The circumpolar boreoarctic bearded seal, *Erignathus barbatus* (Erxleben, 1777), is found as far south as to the White Sea and the Gulf of St. Lawrence in the Atlantic and to the Sea of Okhotsk, even to Sakhalin and Hokkaido, in the Pacific, Occasional stragglers go further south, but the main distribution is at the pack ice in areas with moderate water depths. It moves seasonally with the edge of the ice, but does not perform regular migrations in open water (Scheffer 1958, King 1964). According to Potelov (1966) the bearded seal has been seen close to the North Pole.

Evidence for segregation between age groups has been found by Potelov (1966) and by Burns (1967) who suggests that the tendency to remain near the ice is more fixed in adults than in juveniles.

Two slightly different geographical forms are recognized. These forms have been given the rank of subspecies: *E.b. barbatus* in the Atlantic and *E. b. nauticus* in the Pacific (Scheffer 1958). However, a recent comparative study of more than four hundred crania from the White,

Kara, Barents, Okhotsk and Bering Seas showed no significant differences in growth rates of cranial bones between the different populations (Kosygin and Potelov 1971).

The bearded seal is not a very abundant species, but it is hunted by aborigines all around the Arctic and is quite important in the economy of local communities. World wide catch statistics have not been compiled.

Norwegian sealers have on the average taken some 1 600 bearded seals per year in North Atlantic waters since 1945. About two thirds of these seals were caught by small ships hunting in Svalbard waters and in the northern Barents Sea during summer. However, prices for bearded seal skins have decreased, and in the last few years only occasional catches, mostly taken by expeditions, have been landed.

Annual zones in the cementum and the dentine have been used for age determination in several species of mammals since the technique was described in the early 1950-ies (Laws 1962). In studies of seals a lower canine tooth usually has been selected for ageing, but the method was found to be inapplicable for bearded seals in the Arctic America because the teeth in this species are degenerated and often missing (McLaren 1958, Burns 1967). In those studies the growth ridges on the claws were used for age determination. By this method only a minimum age can be obtained for older seals because wear at the tip of the claw eliminates the first growth ridges after 9 to 16 years (McLaren 1958). However, Potelov (1964) points out that the cementum layers in the upper canines of the bearded seal are useful for age determinations because these teeth have more cementum than lower canines and are not so often missing.

In this paper methods for age determination are studied and data on growth, age distribution, longevity and mortality of bearded seals at Svalbard are presented. Age determinations are based on growth layers in the cementum of the upper canines.

MATERIAL AND METHODS

This study is based mainly on data from 177 bearded seals caught by a sealing vessel in the pack ice of eastern Svalbard waters in May and June 1968. The material was collected by a sealer trained by a technician from the Institute of Marine Research on a previous sealing voyage.

For each animal sex was recorded, the upper jaw collected and the standard length measured along a straight line from tip of nose to end of tail with the animal lying on it's back on a flat surface. Material from 8 and 10 bearded seals collected by biologists in the Barents Sea in the spring of 1968 and at Svalbard in July 1970 has also been examined.

Both the jaw and a claw from the middle digit of one of the fore flippers was collected from 16 of these seals.

Jaws and claws were stored in brine. After boiling for about 30 minutes in water the teeth could be extracted without damage. Inspection of a few longitudinal tooth sections showed that all cementum layers were represented and well defined at about 1 cm from the basal end of the root, and therefore the teeth were cut in transverse sections, 0.1—0.3 mm thick, at this position. The claws were cut in 0.5—0.8 mm thick longitudinal sections. Sections were washed in 96% alcohol, dried and permanently mounted on glass slides with Eukitt (Heinrich Vogel, Giessen).

Cementum layers were most easily counted in a phase microscope, but a binocular microscope could also be used. Growth layers in the claws could be counted by the naked eye.

The annual mortality was calculated by the equation

$$Z = 1 - x / (1 + \bar{x} - 1/n)$$

where

Z = annual mortality
$\bar{x}$ = mean age, beginning with age of full recruitment as zero.
n = number of animals in the fully recruited age groups in the sample,

(Chapman and Robson, 1960).

RESULTS

AGE DETERMINATION

Jaws collected for this study confirm earlier findings by other workers that bearded seal teeth are worn down, degenerate and fall out before the animals are very old. However, the roots of the canine teeth in the upper jaw apparently remain throughout most of the seal's life. Only one out of 194 upper jaws examined, had lost the canine roots.

Because of wear at the tip, length growth of the upper canines stops when the seal is a couple of years old. Canine tooth lengths (straight line distance from tip of crown to tip of root) are shown in relation to age in Fig. 1. A linear rate of tooth wear is suggested although individual differences are clearly indicated.

Dentine deposited in the upper canines during the first year nearly closes the basal opening of the pulp cavity. In the next few years new dentine is added inside the dentine of the first year and does not contribute to the growth of the tooth. The basal opening is closed, the pulp cavity filled, and no more dentine is deposited after the bearded seal

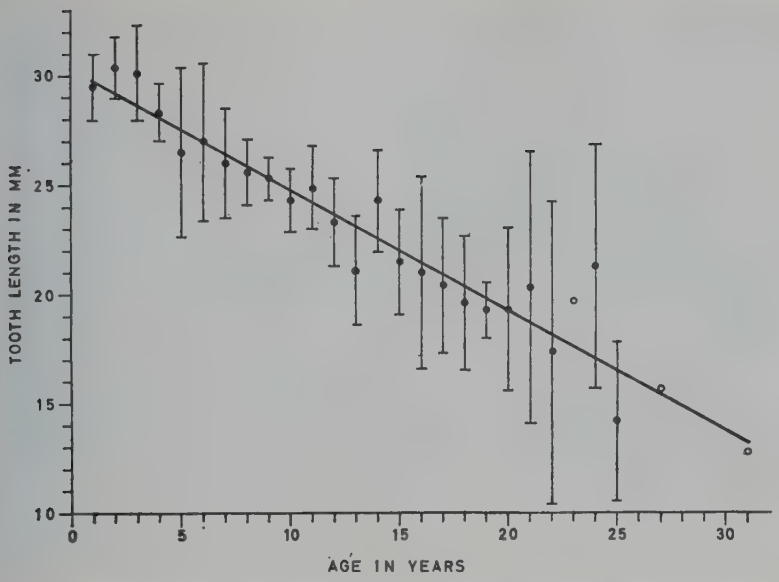

Fig. 1. Lengths of upper canine teeth of bearded seals in relation to age as determined from cementum growth layers. Means and 95 per cent confidence intervals, open circles indicate single measurements. The regression line: $y = -0.55\ x + 30.3$.

is about four years old. Secondary lamination within the annual dentine layers also complicate the interpretation of the layers. Dentine growth layers therefore are not satisfactory as a basis for age determinations.

However, laminated cementum is deposited on the outside of the roots of the teeth as long as they remain in the jaw. The cementum lamina on the upper canines are parallell to the long axis of the tooth, but varying in thickness both around the root and along its length. Lamina can not be distinguished at the basal end of the root.

The cementum of a standard transverse section from an upper canine tooth as is appears in transmitted light is shown in Fig. 2. Alternating translucent and opaque lamina appear as light and dark bands. One light and one dark band together are interpreted as one annual growth layer. Cementum layers usually are sufficiently distinct to be easily counted, but diffuse lamina impeded an exact age determination in about 10 per cent of the sections.

In claws the laminated structure in a longitudinal section is oritented as indicated in Fig. 3.

New lamina are formed underneath and behind the old ones and push the claw forwards while old lamina are removed by wear at the

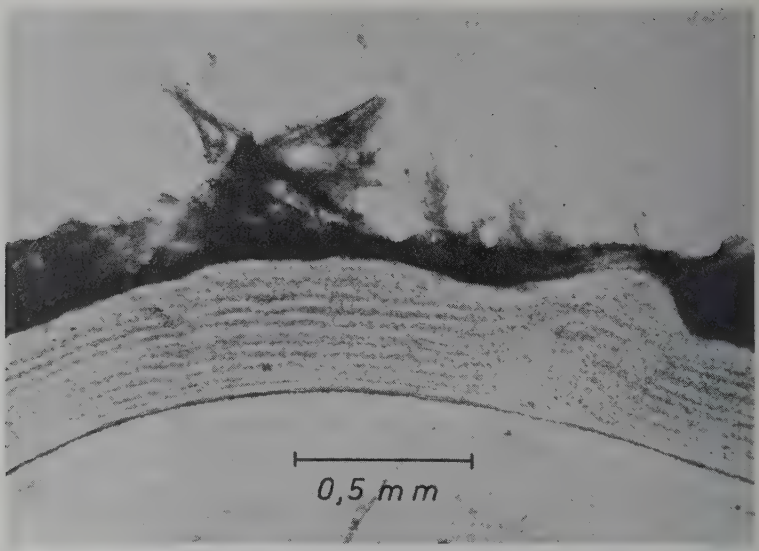

Fig. 2. The laminated structure of cementum in a transverse section from a bearded seal upper canine tooth shown by transmitted light.

tip of the claw as the seal grows older. Part of a longitudinal claw section is shown by transmitted light in Fig. 4. The lamination appears as alternating dark and light bands, one dark and one light band together forming one annual growth layer.

All material used in this study was collected in the spring and summer so the formation of layers in the teeth and the claws could not be followed through the year. However, the relative position of lamina suggests that the light bands in the claws and the opaque lamina in the cementum are deposited during the summer season, and the dark bands and translucent lamina during winter and spring.

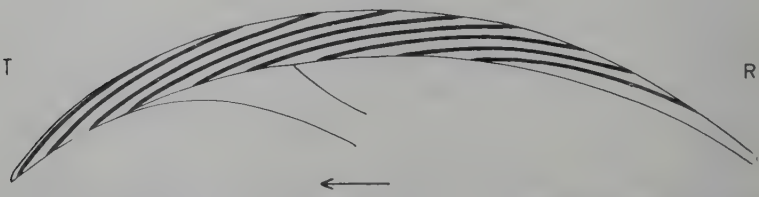

Fig. 3. The orientation of the laminated structure in a longitudinal section of a claw from a bearded seal fore flipper. R)root and T)tip of the claw. Arrow shows direction of growth.

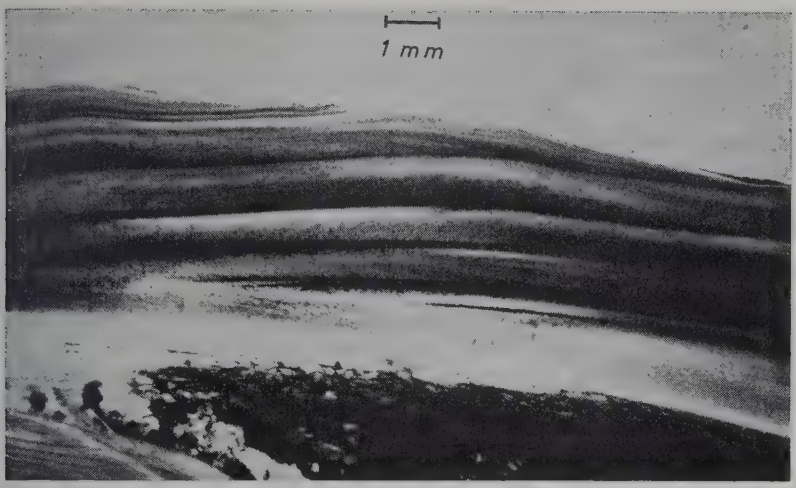

Fig. 4. The laminated structure in a longitudinal section of a claw from a bearded seal fore flipper shown in transmitted light.

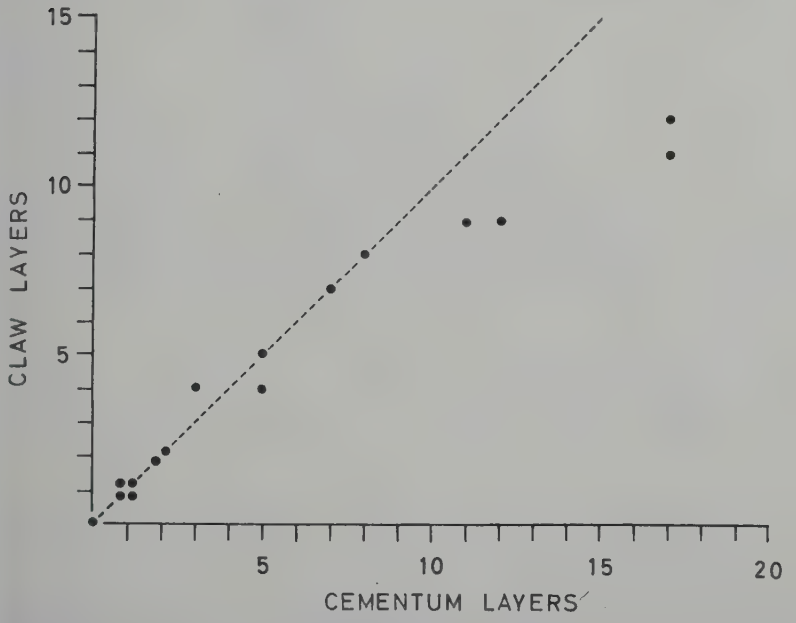

Fig. 5. The number of annual growth layers in the cementum of the upper canine teeth compared to the number of annual layers in claws from 16 bearded seals sampled at Svalbard and in the Barents Sea. The 1:1 relationship is indicated by a broken line.

Age determinations from cementum and claw layers are compared for 16 bearded seals in Fig. 5. Up to an age of about 8 years there is a good correlation between the number of layers in cementum and claws. Two animals — 3 and 5 years old from cementum layers — are exeptions from this rule. In both cases the deviation is explained by obscure bands in the claws. Wear has removed growth layers at the tip of the claw in four 11 years old and older seals.

GROWTH

The relationship between age and standard length for 191 bearded seals is shown in Fig. 6. The mean length at birth (131.3 cm) given by Burns (1967) has been used as a starting point for the growth curve. A mean adult length of 224.7 cm (standard deviation 14.5 cm) is reached at an age of about 10 years. For adult seals 10 years old and older the standard lengths range from 180 cm to 252 cm.

The mean lengths of adult females and males were 226.6 cm and 222.5 cm respectively. A t-test showed that this difference between the sexes was not significant at the 5 per cent level ($t = 1.48$, $0.1 < p < 0.2$).

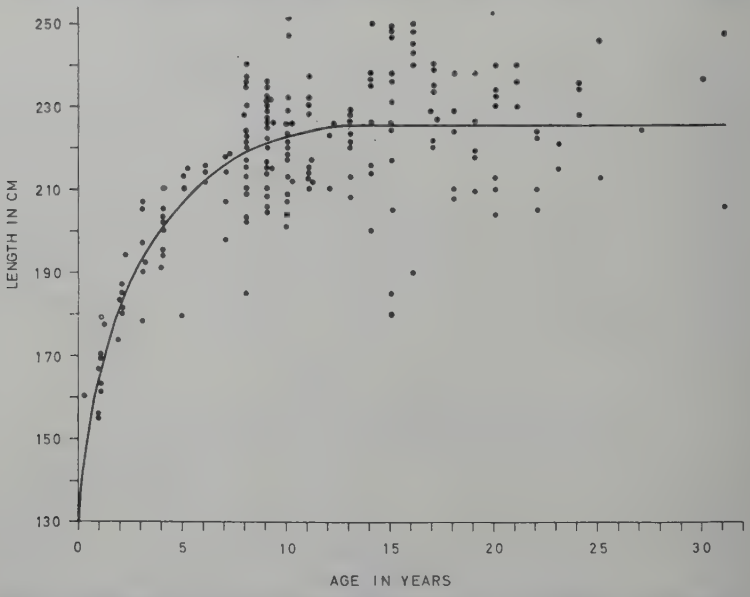

Fig. 6. The growth of bearded seals at Svalbard and in the Barents Sea based on standard length measurements and age determinations from cementum growth layers.

AGE DISTRIBUTION AND MORTALITY

The age distribution as determined from cementum growth layers of 175 bearded seals, all caught in eastern Svalbard waters in May and June 1968, is given in Fig. 7. In this sample age groups are not fully recruited until they are 8 or 9 years old. The oldest male and the oldest female in the sample were 25 and 31 years old respectively.

When 9 years is taken as the age of full recruitment, the total annual mortality rate for 9 years old and older bearded seals in the sample as calculated from the equation

$$Z = 1 - \bar{x} / (1 + \bar{x} - \frac{1}{n})$$

is 0.14.

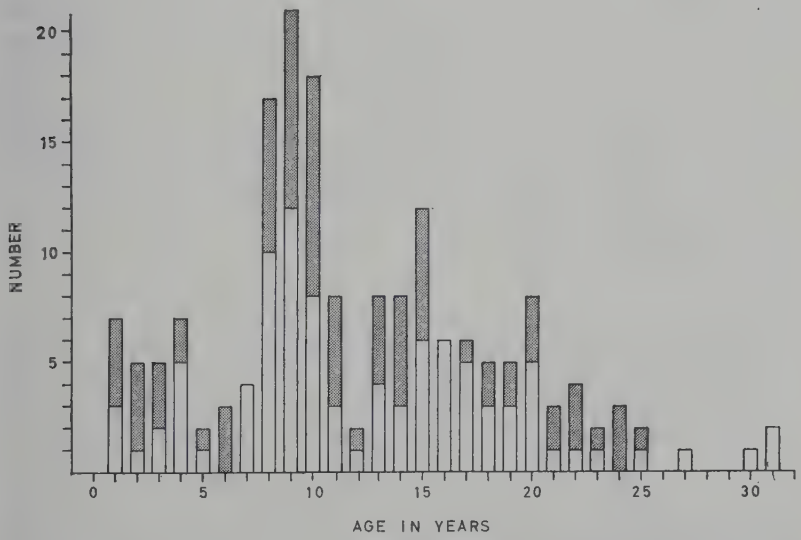

Fig. 7. The age distribution of 175 bearded seals caught in eastern Svalbard waters in May—June 1968. Open columns are females, hatched columns are males.

DISCUSSION

AGE DETERMINATION

The rapid wear and loss of the teeth in bearded seals has been attributed to evolutionary degeneration in tooth structure and to the perhaps conflicting fact that the species is feeding on abrasive benthic invertebrates like clams and crabs as well as ingesting quantities of sand (Potelov 1964, Burns 1967). The discovery that the upper canine

teeth can be used for age determination was first published by Potelov (1964) who concluded that the number of cementum growth layers in these teeth reflects the age of the bearded seal.

Evidence in this study for the annual formation of the cementum growth layers may be found in the close structural resemblace to annual cementum layers in other species (Laws 1962), in the fairly good fit of length data to a normal growth curve (Fig. 6) and in the age distribution of adult seals (Fig. 7).

The growth layers in the claws were found to be deposited annually in bearded seals in Arctic America by McLaren (1958) and Burns (1967) who both studied the surface structure of the claws and found the same pattern of band deposition as indicated by this study. Even if few data are available, the close correlation between the number of growth layers in the claw and in the cementum in young and subadult animals (Fig. 5) therefore gives additional evidence that the cementum growth layers are formed annually.

The deviation between cementum and claw layers in the few adult seals examined (Fig. 5), strongly suggests that studies of age distribution and mortality, perhaps also studies of growth and maturity, should be based on age determinations from cementum growth layers rather than from growth layers in the claws.

GROWTH

McLaren (1968) and Burns (1967) found that the mean length of adult bearded seals in the American Arctic was about 235 cm and 233.7 cm respectively. It is not clearly stated how their measurements were taken, and if zoological lengths were used (measured over curvature of body from tip of nose to end of tail), their data are not strictly comparable to the growth data from this study. A t-test also shows that their mean adult lengths differ significantly from the mean standard length of adults (224.7 cm) found in this study ($t = 2.78$, $p < 0.01$).

In Fig. 6 the lengths plotted for four animals are so much shorter than all others in their age groups that *rigor mortis* contractions may be suspected (one 8 years old male 185 cm, two 15 years old males 180 and 185 cm and one 16 years old female 190 cm). If these animals are omitted from the calculations, the mean standard length of adults changes to 225.8 cm and the range of adult lengths changes to 200 cm—252 cm, but the difference between this mean length and the American Arctic means is still significant at the 5 per cent level ($t = 2.53$, $0.02 < p < 0.03$).

A slightly longer length of adult females than of males (3.1 per cent) was also found by Burns (1967). Omitting the four animals mentioned

above, the mean lengths in this study are 227.3 cm for adult females and 224.1 cm for adult males. The difference is still not significant at the 5 per cent level ($t = 1.23$, $0.2 < p < 0.3$).

AGE DISTRIBUTION AND MORTALITY

The poor representation of age groups from 0 to 7 years in the Svalbard area (Fig. 7) may be explained by a segregation between mature and immature seals in summer. According to Burns (1967) and Potelov (1972 b) female and male bearded seals attain sexual maturity at about five and six years of age respectively. Potelov (1972 a) suggests that bearded seals in the Barents, White and Kara Seas all belong to one population which concentrates in the southern parts of the Barents Sea and the northern White Sea during winter. In summer and autumn the mature seals move north while the immatures and a very few adults remain in the south. A similar pattern of distribution during summer has been demonstrated for bearded seals in the Bering and Chukchi Seas by Burns (1967) who also found a peak at 8—9 years in the age distribution in the Bering Strait during the spring hunting season.

Mortality estimates from the equation used here are based on the following assumptions: 1) Reproduction occurs every year, 2) the number of young born in any year balances the number of seals of all age groups that have died during the previous year, i.e. the population is at equilibrium, 3) the age distribution of fully recruited age groups in the sample represents the age distribution in the population, and 4) the mortality rate is constant in all fully recruited age groups (Chapman and Robson 1960).

Although it has been suggested that females which have recently given birth may forego ovulation until after the mating season and thus establish a two year cycle (McLaren 1958). Burns (1967) found a pregnancy rate of 83—85 per cent among bearded seals in Alaska. A regular one year cycle of reproduction therefore seems likely, and all investigators have found a definite breeding season in late spring (Burns 1967, Potelov 1972 b). The exact timing may differ, but there is a general agreement that young are produced annually.

The other assumptions may be more doubtful. Norwegian catches in the Svalbard area have varied between nil (1967) and 3600 (1951) since 1945 with corresponding changes in hunting mortality. No attempt has been made to assess the influence of hunting on the total mortality of bearded seals at Svalbard or in the Barents Sea, but Norwegian catches have not exceded 600 animals since 1965. It therefore seems

possible that the population nearly was at equlibrium when the sample was collected.

However, there is no reason to believe that natural mortality has changed through the years. Changes in hunting mortality therefore may have influenced the total annual mortality in the population in earlier years.

The small number of specimens in the age sample also makes estimates of mortality somewhat dubious, but most age-groups older than 8 years seem to be fairly well represented. Even with the reservations above which mean that 0.14 can only be used as a provisional estimate of annual mortality, this estimate is called for. Particularly so because no other estimates of mortality are yet available for bearded seals.

It might also be mentioned that decreasing catches at Svalbard and a protection of bearded seals in the southeastern Barents Sea since 1970 (Norwegian—Soviet Sealing Commission) may have produced an increasing survival and a lowered adult mortality in the most recent years.

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M. Fredriksen on the sealer «Blueback» of Tromsø collected the 1968 age and length sample. All material used in this study was put at my disposal by T. Øritsland, Institute of Marine Research, Bergen, who also edited the manuscript.

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OBSERVATIONS ON THE TRANSPORT OF SUGARS IN THE TEMPERATE HOLOTHURIAN, *CUCUMARIA FRONDOSA*

By

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ABSTRACT

Krishnan, S. and Solemdal, P. 1974. Observations on the transport of sugars in the temperate holothurian, *Cucumaria frondosa*. *Fisk. Dir. Skr. Ser. HavUnders.*, 16: 171—176.

Different views have been put forward regarding the function of the perivisceral fluid and coelomocytes in the nutritional transport of echinoderms. To obtain more information in this field an experiment was done with the temperate holothurian, *Cucumaria frondosa*, using carbon labelled glucose, fructose and sucrose. The results showed the main role played by perivisceral fluid in nutritional transport. The different organs such as the alimentary canal, respiratory tree, body wall and gonad showed differences in their uptake.

INTRODUCTION

The roles of the perivisceral fluid and the coelomocytes in the nutritional transport system in different members of the echinoderms have been worked out by other authors (Ferguson 1962, 1963 and 1968; Farmanfarmaian 1963 and 1969; Fontaine and Lambert 1973). However, while considering the role of the perivisceral fluid, some authors (Ferguson 1962, 1963 and 1968; Farmanfarmaian 1963 and 1969) believe that the liquid phase of this fluid plays an important role in the transportation of nutrient materials. In a previous work on a tropical holothurian, *Holothuria scabra* (Krishnan and Krishnaswamy 1970; Krishnan 1971), it was shown that both the perivisceral fluid and the coelomocytes take part in such a function. In the present study *in vivo* experiments were carried out with carbon labelled sugars in the temperate holothurian, *Cacumaria frondosa*, to see the rate of transport of nutrient materials by the perivisceral fluid. The work was also carried out to compare such function in the tropical and temperate forms.

MATERIAL AND METHODS

The specimens of *Cucumaria frondosa* were collected from Strømme near Bergen, Norway, by diving. They were acclimated to the laboratory condition. During the experiments the animals were maintained in continuously circulating sea water with a temperature of 10°C and salinity of 34°/₀₀. Before treating the animals with isotopes, they were starved for not less than 24 hours (to avoid loss through excretion) and then transferred to the experimental tanks. The carbon labelled sugars used in these experiments were purchased from the Radiochemical centre, Amersham, England. These isotopes were first diluted in the filtered sea water to a concentration of 5 μ Ci/ml. Each animal was injected with 1 ml of the above mentioned sugars having the following specific activity:

D-glucose — 1—C—14: 57 mCi per mmol.
D-fructose — 1—C—14: 58 mCi per mmol.
Sucrose — C—14 (U) 600 mCi per mmol.

In order to follow the role of the perivisceral fluid, the radioisotopes were injected directly into the coelom of the animal with the help of a microsyringe. After an interval of 1 hour, 1 ml of the coelomic fluid was syringed out and dissolved in 9 ml of the instagel for counting. To see the rate of uptake of these sugars by different organ systems, major organs such as the alimenteray canal, respiratory tree, gonad and body wall were removed simultaneously from those individuals and dried in a hot air oven at 75°C to constant weight. Each set of experiments (with glucose, fructose or sucrose) lasted for 10 hours. The results given are the mean values of duplicate sets.

For counting the radioactivity in the dry tissues, the method given by the Beckman application, was followed. All the countings were carried out with the Packard Scintillation counter, model 2002. In the case of the perivisceral fluid the results of the translocation are presented in counts per 100 g wet weight of the animal:

$$\left(\frac{\text{counts for 1 ml of the coelomic fluid}}{\text{weight for the animal}} \times 100\right).$$

In the case of the organs the results are expressed in counts per 100 mg dry weight. The results are shown in a semilog graph. Since eye fitting was found more informative, it was used for the perivisceral fluid, and for organs they are plotted using the formula $y = ax + b$.

RESULTS

Fig. 1 shows that all three types of sugars (two mono — and one disaccharide) are translocated, more or less uniformly, from the coelomic fluid. However, the figure also shows clearly that glucose and sucrose are transported much more quickly than fructose. It is also obvious that such a function is completed within the first 4—5 hours for all the sugars.

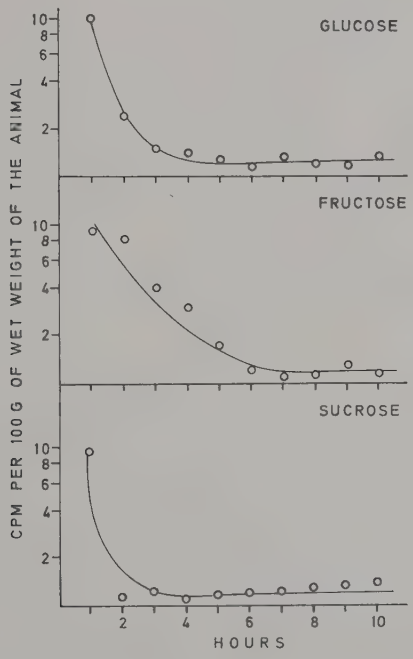

Fig. 1. The rate of translocation of carbon labelled sugars by the perivisceral fluid during 10 hrs. Actual values in Y-axis: 2×10^4 for glucose; 4×10^3 for fructose and sucrose.

Of the four major organs analysed (namely body wall, alimentary canal, respiratory tree and the gonad) for the uptake of the translocated sugars from the perivisceral fluid, the body wall appears to have absorbed a maximum of glucose when compared to other organs (Fig. 2 A); the respiratory tree seems to have taken up mainly fructose (Fig. 2 B); the alimentary canal seems to have absorbed all the sugars in the beginning, but started losing glucose and fructose after some time (Fig. 3 A). In the case of the gonad all three sugars are absorbed in the beginning, but after some time it starts losing all of them (Fig. 3 B). Such diversified results may be due to the varied metabolic stage of the organs.

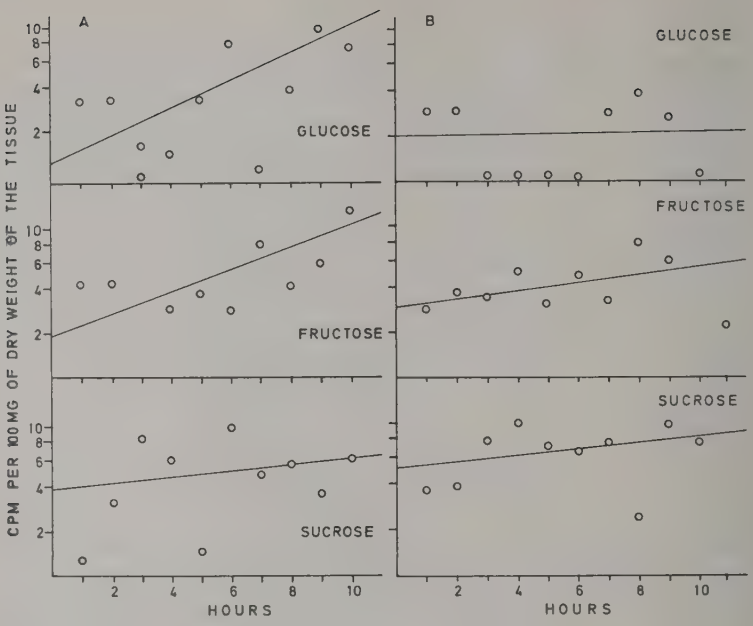

Fig. 2 A. The reaction of the body wall to the C-14 sugars.
$Y = 2091x + 0{,}31$ for glucose
$Y = 1077x + 0{,}44$ for fructose
$Y = 551x + 0{,}95$ for sucrose

Fig. 2 B. Absorption rate of carbon labelled sugars by the respiratory tree.
Actual values in Y-axis: x 10^5 for glucose, x 10^4 for sucrose and fructose.
$Y = 979x + 0{,}20$ for glucose
$Y = 2189x + 0{,}29$ for fructose
$Y = 2736x + 0{,}52$ for sucrose

DISCUSSION

The results of the present experimental studies confirm the view of Farmanfarmaian (1963) and Krishnan (1971) that the perivisceral fluid is playing a significant role in the transport of both of the sugar types employed. While presenting the rate of uptake of sugars in the holothurian, *H.scabra*, Krishnan and Krishnaswamy (1970) found that there appeared to be selective absorption of the sugars by different organs analysed. In *C. frondosa*, experiments with the labelled sugars have shown such selective absorption by the various tissues. However, such selectivity differs from what was observed for *H. scabra*. In the present study there seems to be a loss of the absorbed sugars from the

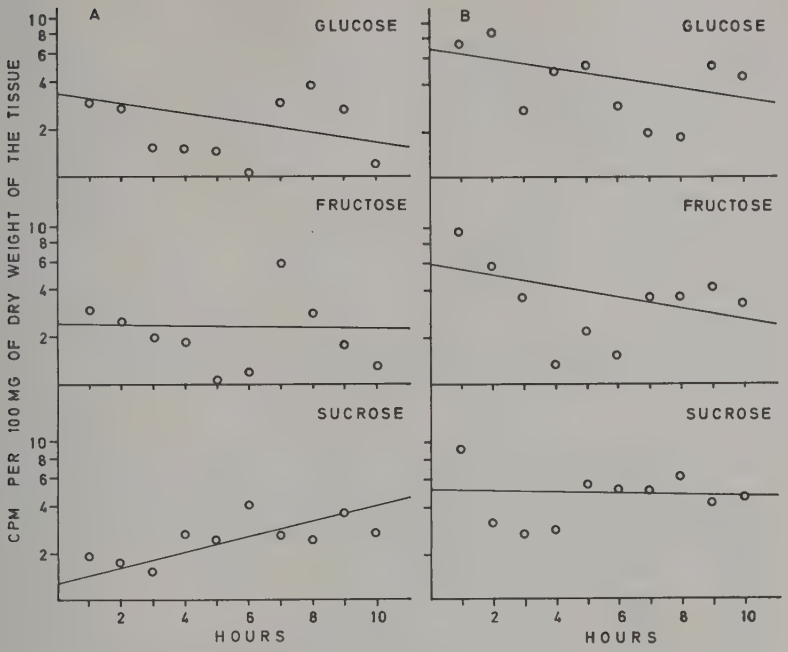

Fig. 3 A. The rate of absorption of C-^{14} sugars by the alimentary canal.
Actual values in Y-axis: x 10^4 for all sugars
$Y = -1713x + 0{,}32$ for glucose
$Y = -238x + 0{,}24$ for fructose
$Y = -2158x + 0{,}13$ for sucrose.

Fig. 3 B. Absorption rate of C-^{14} sugars by the gonad.
Actual values in Y-axis: x 10^3 for glucose; 5×10^3 for fructose; $3{,}5 \times 10^2$ for sucrose.
$Y = -401x + 0{,}67$ for glucose
$Y = -1938x + 0{,}30$ for fructose
$Y = -239x + 0{,}18$ for sucrose

alimentary canal. This is true for the monosaccarides glucose and fructose. However, sucrose is shown to be steadily increasing with time. In another holothurian, *Thyone briareus*, Farmanfarmaian (1969) reports that the little glucose absorbed (3—17%) in the beginning was later transferred to the required organs through the perivisceral fluid by active transport. This too is true in the case of *C. frondosa*.

While looking into the uptake of sugars by the respiratory tree and body wall, one can easily understand that all those sugars were absorbed steadily. However, the body wall appears to be utilizing more of the monosaccharides than the disaccharide. It is shown in different species of holothurians that glycogen is absent in the body (Benazzi-Lentati

1941; Fish 1967; Krishnan 1968). Hence it is tentatively suggested that the body wall may be utilizing the simple sugars available, instead of the glycogen, for its metabolic activity. On the other hand the respiratory tree seems to have more capacity for utilizing sucrose when compared to the other organs. It is quite obvious that this being the most active organ of the body, it is able to utilize all the sugars, sucrose in particular.

The animals taken for the experiments were all in mature condition. It is suggested that since there may not be much synthetic activity in mature gonads, no significant uptake of sugars has been shown by the gonadal tissues. Further, the descending nature of the slope in the regression lines for the three sugars (Fig. 3 B) can be explained as the reabsorption by the coelomic fluid and translocation to other active organs like the respiratory tree and body wall.

ACKNOWLEDGEMENTS

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COMPARISON OF BLOOD PROTEINS OF COALFISH FROM NORWEGIAN AND ICELANDIC WATERS

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ABSTRACT

Møller, D. and Nævdal, G. 1973. Comparison of blood proteins of coalfish from Norwegian and Icelandic waters. *FiskDir. Skr. Ser. HavUnders.*, *16*: 177—181.

Blood samples of coalfish from Norwegian and Icelandic waters were collected and analyzed for hemoglobin, serum protein, and serum esterase variations in order to study the relation between the two coalfish stocks. Clear intraspecific variation was found in the serum transferrins, but the distributions of phenotypes were nearly the same in the sample from Iceland as in the total samples from Norwegian waters.

INTRODUCTION

The coalfish, *Pollachius virens*, spawns on the banks off the west coast of Norway and in the northern North Sea. Other spawning grounds are located at Iceland and the Feroe Islands. The three stocks of coalfish have been regared as separate selfsustaining populations, but tagging experiments have shown a rather extensive emigration from Norway to Iceland and Feroe waters (Olsen 1961).

In the investigations reported here an attempt have been made to use frequencies of polymorphic or Mendelian characteristics to study the relation between coalfish from Norwegian and Icelandic waters. The electrophoretic patterns from analyses of coalfish hemoglobins are described elsewhere as a part of a comparative study on hemoglobins of gadoid fishes (Møller and Nævdal 1969).

MATERIAL AND METHODS

Numbers of specimens in each sample, sampling date and sampling localities are shown in Table 1. The Norwegian sampling localities are also plotted in Fig. 1. Samples 1—3 were collected from coalfish brought alive for commercial sale at Bergen harbour, and detailed catching localities are unknown. Samples 7 and 12 were collected from fishes of the O-group, and samples 8 and 10 were collected from mature fishes (sample 8 in the spawning season). All the other samples were collected from one to three years old immature fishes.

Fig. 1. The location of the Norwegian sampling stations listed in Table 1.

Bloods were collected by cardiac puncture or by cutting the tail (small fishes). Samples 1—6 and 12 were analyzed for hemoglobin variation, and in the these samples heparin was used as anticoagulant. The hemoglobins were analyzed fresh, but most sera were stored for some days or weeks in a deep freeze before analyses.

The hemoglobins were analyzed by agar gel electrophoresis (Sick 1965). Sera were analyzed by the combined starch and agar gel electrophoresis described by Møller (1966). The proteins were stained by Amidoblack 10 B or Nigrosin. Autoradiography was carried out as for cod sera (Møller 1966) based on the method of Giblett, Hickman and Smithies (1959). Staining of esterase activity was performed by 1 % napthylacetate in aceton using Fast Blue BB Salt as dye coupler.

RESULTS AND DISCUSSION

The hemoglobin analyses did not reval any individual variation in coalfish, except one single specimen which showed two strong fractions while all the other specimens analyzed showed only one strong fraction (Møller and Nævdal 1969). As intraspecific variations were very rare, further studies on hemoglobins of coalfish were omitted.

Also the results of esterase analyses were discouraging as only a diffuse area of esterase activity with no clear intraspecific differences was found.

Serum protein variation of coalfish has been briefly dealt with in preliminary reports (Møller and Nævdal 1966, Møller, Nævdal and Valen 1967).

Some serum protein electrophoretograms are outlined in Fig. 2. A strong fraction of intermediate anodic mobility was shown by autoradiography to represent serum transferrins and was named Tf A. Tf A occurred in all specimens analyzed. Also the weaker component in front of it was found to possess ironbinding capasity. In a few per cent of all specimens analyzed another strong component occurred at the cathodic side of Tf A, and in two specimens (one in sample 8 and one in sample 12) a corresponding strong component occurred at the anodic side of Tf A, also this component with a weaker component in front of it. Sera in which these components occurred were not available when the tracing experiments were made, but their strength and position imply that they represent rare transferrin components, and they were named Tf B and Tf A' respectively. The phenotype which contained Tf A alone, was named Tf AA, and the phenotypes in which Tf B and Tf A' occurred, were called Tf AB and Tf AA' respectively.

The distribution of the phenotypes Tf AA and Tf AB in the collected

Table 1. Observed distributions of transferrin phenotypes in samples of coalfish from Norwegian and Icelandic waters with calculated gene frequencis and expected Hardy-Weinberg distributions.

Sample no	Locality	Date of sampling	Transferrin type			Numbers in sample	Gene frequency q_B
			TfAA	TfAB	TfBB (exp)		
1	Hordaland	4 Aug. 1965	97	3	—	100	0.015
2	Rogaland	11 » 1965	57	3	—	57	—
3	Hordaland	16 Dec. 1965	108	4	—	112	0.018
4	Smøla, Nordmøre	16 » 1965	108	3	—	111	0.014
5	Sandøy, Romsdal	16 » 1965	86	4	—	90	0.022
6	Veidholmen, Nordmøre	17 » 1965	38	—	—	38	—
7	Gamsvik, Vestfjorden	26 Sept. 1965	13	—	—	13	—
8	Røstbanken	8 March 1966	157	6	—	163	0.018
9	Husøy, Nordland	8 Aug. 1966	93	2	—	95	0.011
10	61°00N, 03°E' Viking Bank	22 » 1967	79	3	—	82	0.018
11	Borgenfj. Trøndelag	25 Oct. 1967	20	1	—	21	0.024
	Total, Norwegian waters		856	26	—	882	0.0157
	Expected Hardy-Weinbergs distribution		856	25	0.2		
12	Husavik, North-Iceland	13 Aug. 1967	190	10	—	200	0.025
	Expected Hardy-Weinberg distribution		190.1	9.8	0.1		

samples are shown in Table 1. The numbers of Tf AA' are lumped with the numbers of Tf AA.

A hypothesis of genetic control of the transferrings involving two co-dominant alleles, Tf^A and Tf^B, has been adopted to explain the observed variation. In Table 1 the frequencies of Tf^B are calculated for each sample, and expected distributions of genotypes are calculated for the total of Norwegian samples and for the sample from Iceland respectively. The expectance of the genotype Tf^B/Tf^B in the present material is low, and the overall accordance between observed and expected distributions is reasonable good, implying that the hypothesis is correct.

TfA' may have a similar control, but because this component is very rare, this hypothesis can not be tested from population data.

Also in other serum proteins intraspecific variations were observed (Fig. 2), but they occurred as presence or absence of weak fractions and clear-cut typing of the individual specimens was impossible.

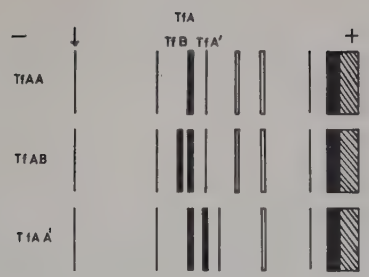

Fig. 2. Outline of serum protein patterns in coalfish obtained by combined starch and agar gel electrophoresis at pH 0.9.
Filled in bars: Strong bands. Open bars: Moderately strong bands. Hatched bars: Diffuse bands. Single lines: Faint bands. Arrow indicate the point of application.

Table 1 shows that no great differences were found among the samples in distribution of transferrin phenotypes. The q^B-value varied between zero and 0.024 in the Norwegian samples, but showed a somewhat higher value, 0.025, in the sample from Iceland. However, χ^2 homogenity test on the distribution of phenotypes showed that the difference between the Norwegian and the Icelandic samples was not significant $\chi^2 = 2.14$, 1 d. f.,$0.1 < P < 0.2$).

Thus no significant difference between Norwegian and Icelandic coalfish was detected in the present study. This may imply that the two stocks are not genetically isolated, but the reason may also be that the transferrin variation is a balanced polymorphism where the controlling factor (probably one or another abiotic ecological factor) shows so similar values in the two environments that similar gene frequencies are established.

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COMPARISON OF BLOOD PROTEINS FROM EAST AND WEST ATLANTIC POPULATIONS OF *HIPPOGLOSSOIDES PLATESSOIDES*

By

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ABSTRACT

Nævdal, G. and Bakken, E. 1974. Comparison of blood proteins from east and west Atlantic populations of *Hippoglossoides platessoides*. *FiskDir. Skr. Ser. HavUnders.*, *16*: 183—188.

Hemoglobins, serum proteins and serum esterase of *Hippoglossoides platessoides* from the eastern and western part of the North Atlantic were analyzed by gel-electrophoresis. Great variety were observed among specimens, and a few rare phenotypes were found only among representatives of one of the two areas. Most phenotypes, however, were found both in the east and west Atlantic samples, although they occurred at different frequencies. The observed differences give no basis for regarding the east and west Atlantic populations as separate species.

INTRODUCTION

Norman (1934) divided the species *Hippoglossoides platessoides* (Fabricius) in the North Atlantic into two subspecies, each with its own geographical range: *H.p. limandoides* (Bloch) in northwestern Europe and *H.p. platessoides* (Fabricius) in North America. He points out, however, that the European and American forms, called long rough dab and American plaice respectively, intergrade in areas where their ranges overlap. Specimens from Iceland and Spitzbergen, for example, approach the American subspecies in depth of body, number of scales, etc.

H. platessoides is only lightly exploited but may be regarded as a potential fish resource both on the east and west side of the North Atlantic. For management purposes criteria for distinction between possible stock units will be of significance.

The purpose of the investigations reported here has been to study the relation between the two subspecies by use of characteristics of some blood proteins.

MATERIAL AND METHODS

An account of the collected material is given in Table 1.

Samples of the fish were selected to cover the entire size range. Bloods were obtained by cutting the tail or drawn by syringe from the heart.

Table 1. Samples of *Hippoglossoides platessoides* analyzed for blood protein variations.

Sample no	Locality and date	Length range, cm	Specimens analyzed		
			Hemoglobin	Serum proteins	Serum esterase
1	St. Margaret's Bay, N.S., Canada Apr '68	28—53			14
2	— Oct '68	29—59	73	73	73
3	59°20'N 04°00'E, North Sea Aug '68	12—20	60	10	51
4	72°00'N 30°00'E, Barents Sea May '70	25—40		90	90

Samples from Canada were shipped by air to the Institute of Marine Research, Bergen and received within two days. Sample 1 was sent as whole bloods, but this caused lysis of the blood cells, and the sample was suitable only for analyses of serum esterase. In sample 2 sera were separate from the cells before shipping, and both sera and cells were received in good conditions.

Sample 3 was collected onboard a trawler and sent to the Institute where it was received the next day. Sample 4 was collected onboard R.V. "Johan Hjort". This sample had to be kept in the deep freeze until the ship returned to Bergen, and because fish hemoglobins withstand freezing poorly, only sera were analyzed.

Hemoglobins were analyzed by agar-gel electrophoresis at pH 7.2 as described by Sick (1965). Sera were analyzed by the combined starch and agar-gel electrophoresis described by Møller (1966) and stained for general protein patterns by Nigrosin and for esterase activity by α-naphtylacetate with Fast Blue BB Salt as dye coupler.

Hemoglobins were analyzed fresh while sera were analyzed both fresh and after being kept in the deep freeze for several months.

RESULTS

HEMOGLOBINS

The observed hemoglobin patterns are outlined in Fig. 1 A.

Two strong and one weak band, pattern 1, were found for all specimens, except four which had individual patterns. Patterns 2 and 3 were found in the sample from the North Sea while 4 and 5 were found in sample 2 from Canadian waters.

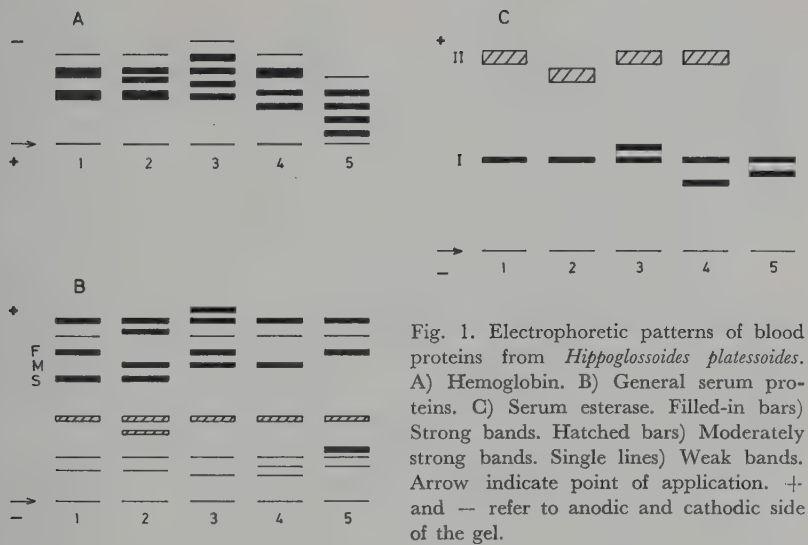

Fig. 1. Electrophoretic patterns of blood proteins from *Hippoglossoides platessoides*. A) Hemoglobin. B) General serum proteins. C) Serum esterase. Filled-in bars) Strong bands. Hatched bars) Moderately strong bands. Single lines) Weak bands. Arrow indicate point of application. + and − refer to anodic and cathodic side of the gel.

The observed variation may be genetically controlled, but this hypothesis can not be tested on the present material due to the scarsity of other phenotypes than the "normal" one.

GENERAL SERUM PROTEINS

Some typical patterns of general serum proteins are outlined in Fig. 1 B. A high degree of variation among individual specimens was found within all samples.

The proteins of highest anodic mobility, the albumins, were seen as a single band in most specimens, sometimes with a weak postalbumin at its cathodic side. Double albumins, patterns 2 and 3, occurred at low frequencies both in samples from the west and east Atlantic.

At least three strong bands, called F(ast), M(iddle) and S(low), occurred at the cathodic side of the albumins. In all specimens one or two of these bands were seen, indicating control by three (or more) allelic genes. However, these bands were not always clear enough to permit calculations of frequency distributions of the phenotypes, and thus the hypothesis of genetic control could not be tested. The S band occurred at considerably lower frequency in the samples from the east compared to the west Atlantic.

Individual variations, probably genetically controlled, were observed in several groups of weak components with low anodic mobility.

Due to the weakness of the bands, grouping of the individuals on the basis of their variations was impossible.

In the sample from the Barents Sea one strong component occurred in some specimens; pattern 5. This band may represent the "ripe female protein" noted in other species (Nævdal 1969, Tsuyuki and Roberts 1966).

SERUM ESTERASE

The patterns of esterase activity are outlined in Fig. 1 C.

In the Canadian samples two main zones of esterase activity, called I and II, occurred. In two specimens the II band was lacking. In the samples from the east Atlantic the II band was observed in only four specimens. When the II band occurred, it was found at the same position as in the Canadian samples, except in one specimen where it was found to possess somewhat lower anodic mobility; pattern 2.

Three different variations of double I bands were found; patterns 3, 4 and 5. Three specimens of sample 2 and one specimen in each of samples 3 and 4 showed an extra band at the anodic side of the normal I band. Extra bands at the cathodic side of the normal I band were seen at two positions. The slower moving band, pattern 4, was found in one specimen of sample 1 and five specimens in each of samples 3 and 4. An extra band of somewhat higher mobility, pattern 5, was only found in two specimens of sample 4.

A genetic system of four alleles would explain the observed variation of the I band, but scarsity of the variants, hypothetical heterozygotes, prevents this hypothesis from being tested by population data.

DISCUSSION

Two populations are said to be conspecific when they are actually or potentially inbreeding (Mayr, Lindsley and Usinger 1953). The populations of *H. platessoides* from the east and west Atlantic are geographically isolated and consequently not actually inbreeding. The problem of their conspecific nature therefore is reduced to determine whether they are potentially inbreeding.

In the present study the genetic basis of the observed variation has not been worked out in details. Bur no indications of growth dependent variation were found, and sex dependent variation was only indicated in one serum protein of low anodic mobility. The possibility exists that modifications caused by factors other than genetic may account for part of the observed variations. However, the genetic basis of the protein structure (Peacocke and Drysdale 1965) strongly signify that analyzes of charac-

teristics of the proteins are useful for discrimination of the genotype of individuals and populations.

The east and west Atlantic populations did not differ to a great extent. In the characteristics studied here some hemoglobin and serum esterase I phenotypes were found among representatives of one population only. All these phenotypes were rare, and analyses of greater material would possibly show that they exist also in the other population.

The greatest difference was found in the esterase II component which was lacking in most specimens from the east Atlantic. However, some specimens contained this component as well as it infrequently was lacking in the west Atlantic samples. The varied occurrence of esterase II is thus merely a difference in frequency distribution of phenotypes. Such differences were also observed in distributions of some esterase I components and serum protein components.

The two subspecies, as established by NORMAN (1934), differ in some morphological and physiological characters. In European waters (Clyde area) the maximum length is about 30 cm at 6 years of age (BAGENAL 1955) while it is about 68 cm and 26 years in Canadian waters (POWLES 1965). The fecundity or rate of egg production in relation to size and age is remarkably similar (PITT 1964), but the females of the European form mature at much smaller size and at much younger age than the American form.

Such physiological variance are commonly found between fish subspecies and correspond to the differences observed in the present investigation of blood characteristics. These differences are of a type which should be expected between conspecific populations rather than between species.

The results of the present study have not excluded that the east and west Atlantic populations of *H. platessoides* is potentially inbreeding, and until greater differences in their genotypes are revealed, they should be regarded as conspecific.

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A TECHNIQUE FOR SECTIONING BLUE WHITING OTOLITHS FOR AGE DETERMINATION

By

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ABSTRACT

Jakupsstovu, S. H. í. 1974. A technique for sectioning blue whiting otoliths for age determination. *FiskDir. Skr. Ser. HavUnders.*, *16*: 189—193.

The basic principle of the method is to embedd the otoliths in a two component glue whereafter it is sectioned with a jewelers saw. When using this method a trained technician can section and make age determinations of approximately 50 otoliths per day.

INTRODUCTION

Age determination on blue whiting, *Micromesistius poutassou* (Risso, 1810), is most successfully performed by counting alternating hyaline and opaque zones in the otoliths (Raitt 1968).

The method commonly used in examining blue whiting otoliths is that discribed by Gambell and Messtorff (1964) for whiting otoliths. The otolith is broken transversely, and a beam of light striking the side of it is transmitted upwards through it, illuminating the hyaline and opaque zones on the broken surface. When working on blue whiting from the Norwegian Sea and adjacent areas this method was found to be difficult in obtaining reliable age determination of fish older than 5—7 years. The reason for this is that the outer opaque zones in old fish are very thin, and a great proportion of the fish form secondary rings in the otoliths. When sending the light in from the side the illumination of the surface is in many instances insufficient to distinguish primary rings from secondary rings, and the contrast is too weak to permit a sufficient discrimination of the zones.

In order to obtain better contrast in the otoliths, burning (Christensen 1964) and dying (Albrechtsen 1968) the otoliths has been tried without success. Sections are the only means by which the internal structure of some otoliths can be seen (Johnston 1938). The main objections against sectioning otoliths is the time used for preparation of sections. In the search for an efficient method a modification of that described by

TÅNING (1938) for cutting cod otoliths has been adopted. This is a fairly rapid method and a trained technician can prepare and determine age of about 50 otoliths per day.

THE METHOD

The basic principle of this method is to embedd the otolith in a plastic glue whereafter it can be cut into sections with a saw. The embedding medium used is a two component glue (Araldit, manufactured by A/S Sigurd Hesselberg, Oslo). This gives a firm grip on the otolith and prevents breaking of the sections when sawed.

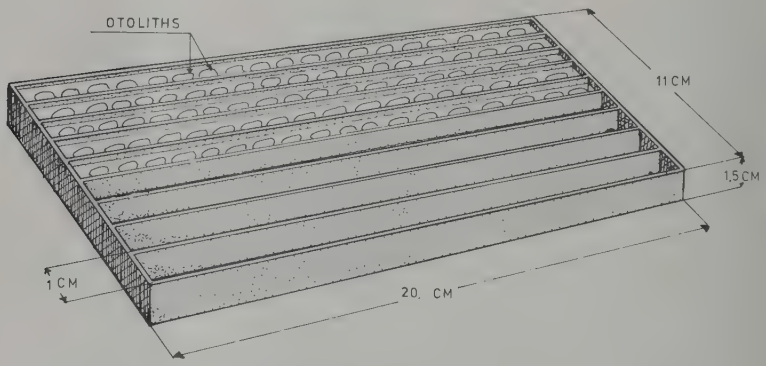

Fig. 1. Sketch of the tray-mould used for embedding the otoliths.

For practical reasons a special tray-mould has been made for the embedding (Fig. 1). This is made of metal and divided into 9 compartments, each giving room for 12—15 embedded otoliths. Before embedding the inside of the mould is covered with a thin layer of paraffin wax in order to prevent the glue from sticking to it. After this a ground layer (1—2 mm thick) of Araldit is placed in the form and allowed to dry for 1—2 hours at room temperature. The glue is then stiff enough to prevent the otolith from sinking, and at the same time it holds the otoliths when they are finally covered with glue.

A 1—3 mm thick cover of glue is sufficient to hold the otoliths during sawing, and when using this thickness the otoliths are fully visible, making it possible to section any desirable place of the otolith.

When the glue is dry (24—48 hours at room temperature, earlier if heated), the mould is heated to above the melting point of the paraffin.

The blocks of Araldit with the embedded otoliths can then easily be taken out, and in this form they can be kept indefinately.

The sectioning is done with a jewelers saw. The best results have been obtained with steel blades 0.2 mm thick and with 20.3 teeth per cm. Good results have also been obtained with thicker blades, but the disadvantage with these are that a greater part of the otolith is lost during sectioning.

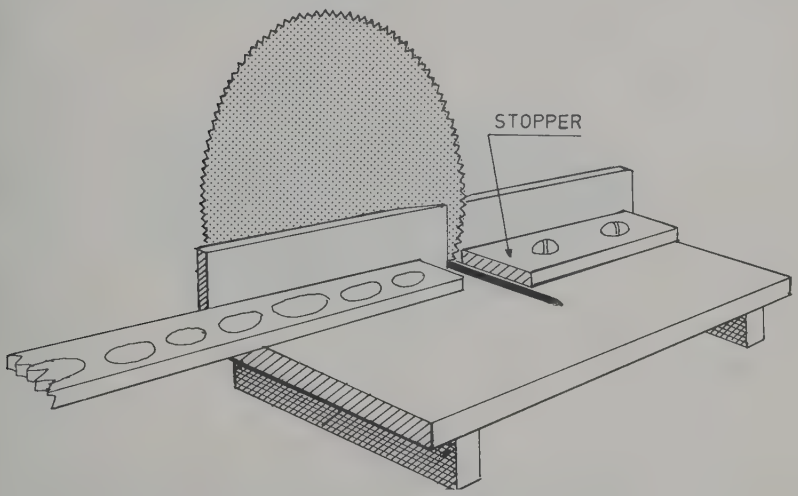

Fig. 2. Sketch of the tray and saw used when the otoliths are sectioned.

The embedded otoliths are placed on a tray with an adjustable stopper (Fig. 2) and held firmly by hand. By moving the tray against the rotating blade sections down to 0.3 mm can be made. The preferred thickness is form 0.4—0.6 mm.

Blue whiting has large otoliths with a wide first zone, and 2—3 sections can usually be made from the centre area without losing any zones. The sections are then washed in alcohol, which also acts as a clearing agent, and mounted in Eucit on glass slides.

The reading can be done immediately by binocular microscope with transmitted light from below, using a grey filter. A better result is obtained with a polarisation filter which makes it possible to change the angles of the light waves against the zone walls.

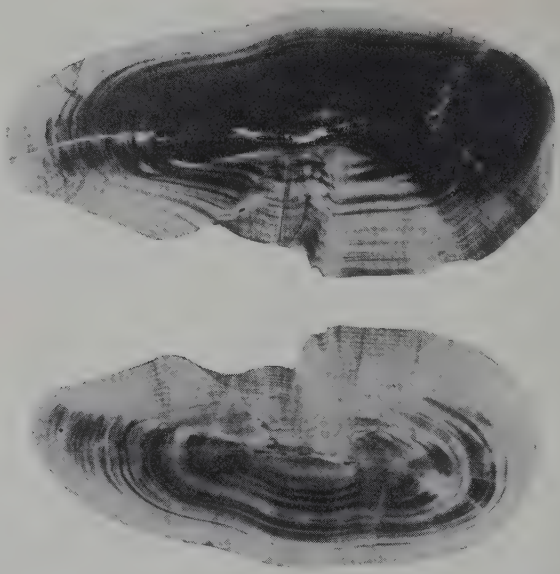

Fig. 3. Sections from blue whiting otoliths. Top) Female 32,5 cm. Bottom) Female 33,5 cm.

RESULTS

So far, the results of the sectioning seem very promising. Sections have been made from several hundred otoliths, and age determinations have been possible for otoliths formerly assigned as unreadable or uncertain. Fig. 3 illustrate sections from two otoliths.

The method has also been tried on otoliths of polar cod with good results.

ACKNOWLEDGEMENT

The method is based on equipment used for sectioning seal teeth, and I am indebted to T. Øritsland and B. Bergfløt for their kind help. Special thanks is due to K. A. Larsen who has prepared and photographed the sections and H. Kismul who has drawn the illustrations.

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ON THE HYDROGRAPHIC FLUCTUATIONS IN THE LABRADOR SEA DURING THE YEARS 1959—1969

By

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ABSTRACT

Blindheim, J. 1974. On the hydrographic fluctuations in the Labrador Sea during the years 1959—1969. *Fish. Dir. Skr. Ser. Hav Unders., 16*: 194—202.

During the years 1959—1969 Norwegian fishery research vessels collected oceanographic data off West Greenland, the observational work mainly being done in April. The data reveal gradually falling temperatures in the upper layers because of increasing supply of Arctic water to the West Greenland Current during the 1960s. The reason for this seems to be the atmospheric pressure and wind conditions which also were in favour of an offshore drift of the surface waters along the West Greenland coast.

Between the surface waters of Arctic characteristics and the Irminger water below vertical convection was to a great extent prevented by a transition layer of high stability. The radiant heat loss during the winter season was, therefore, limited to the upper layers, adding to the decrease in temperature created by the growing supply of Arctic water. In waters of salinity below 34‰ in the section across the Fylla Bank the temperature fell by 1.6°C during the period.

The trend in the Irminger water was different, and the temperature in this water mass rose until 1966.

The cooling in the upper layers can be traced down to approximately 400 m depth, but it was most pronounced at 100 to 150 m depth off the edge of the shelf where the temperature fell by about 2°C. At depths below 400 m the warming effect of the Irminger water can be traced down to 1 000 to 1 200 m depth.

INTRODUCTION

In West Greenland waters where some important fish species find the poleward border of their range, these species are particularly sensitive to environmental fluctuations. This was clearly demonstrated at the beginning of the last good cod period on the West Greenland fishing banks when a marked temperature increase was observed. The longest series of oceanographic observations in the area are sea surface temperatures collected for the Danish Meteorological Institute since 1876. As shown by Smed (1965) these observations indicate a marked tempera-

ture increase in the 1920s. The warming continued until the beginning of the 1930. Since then the temperature has on an average remained above the mean for the 40 year period 1876—1915 until recently.

The biological consequences of this temperature increase is described by Jensen (1939), the best known and most important being the northward extention and strongly increased abundance of the cod stock. The capelin in the area showed an opposite reaction as the southern limit of its range shifted northwards.

Since the beginning of the 1960s a cooling trend has been observed, and the temperature in the surface layer is now about the same as it was before 1920, and its unfavourable effect on the cod stock is already being observed. The reason for this is a general climatic deterioration over the Northwest Atlantic and the European Arctic. This hydro-meteorological fluctuation has in particular been studied by Rodewald (1967, 1969, 1971), and he shows that since the 1950s the atmospheric pressure in the Greenland high has been above normal. This has given rise to anomaly northerly winds over the Greenland and Norwegian Seas, and consequently to a temperature decrease in this area. It has also given rise to increased transport of Polar water to the East Greenland Current, and as described by Malmberg (1969), also to the East Icelandic Current. In the North Atlantic south of Iceland and in the Irminger Sea the anomaly pressure and wind have caused an increased supply of Atlantic water to the Irminger Current. Off West Greenland the atmospheric conditions brought about an offshore drift of the surface waters which resulted in an abnormal great lateral extent of the Arctic Component of the West Greenland Current. As reported on by Blindheim (1967) this is demonstrated by observations made on Norwegian fishery research vessels which surveyed the area during the spring of the years 1959—1969. After 1969 these investigations were discontinued and the present paper is, therefore, based on the complete series of hydrographic data from these cruises.

MATERIAL AND METHODS

The hydrographic data consists of temperature and salinity observations made with Nansen casts. Most of them are collected in late March or in April, and some few in the first days of May. Mainly due to ice obstacles, the station grid varied somewhat from year to year. In general, however, the intention was to work sections perpendicular to the coast across the more important fishing banks. As an example the grid of stations worked in 1966 is shown in Fig. 1. The number of stations worked in the sections across the banks in the different years are compiled in Table 1.

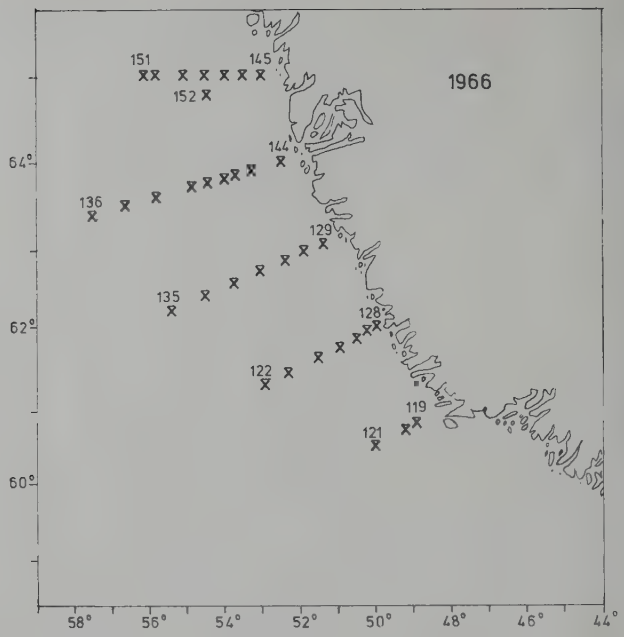

Fig. 1. Grid of stations worked in 1966.

Table 1. Number of hydrographic stations worked in the different sections across the fishing banks off West Greenland in the years 1959—1969.

Year	Fredriks-håb Bank	Danas Bank	Fyllas Bank	Lille Hellefiske Bank	Other	Total
1959 ...	4	8	8	8	10	38
1960 ...	5	5	5	5	8	28
1961 ...	7	7	7	7	25	53
1962 ...	4	0	5	5	2	16
1963 ...	6	0	9	5	7	27
1964 ...	7	6	6	5	15	39
1965 ...	6	5	9	6	9	35
1966 ...	7	7	9	7	4	34
1967 ...	7	7	5	4	6	29
1968 ...	5	7	9	7	5	33
1969 ...	0	7	8	6	4	25

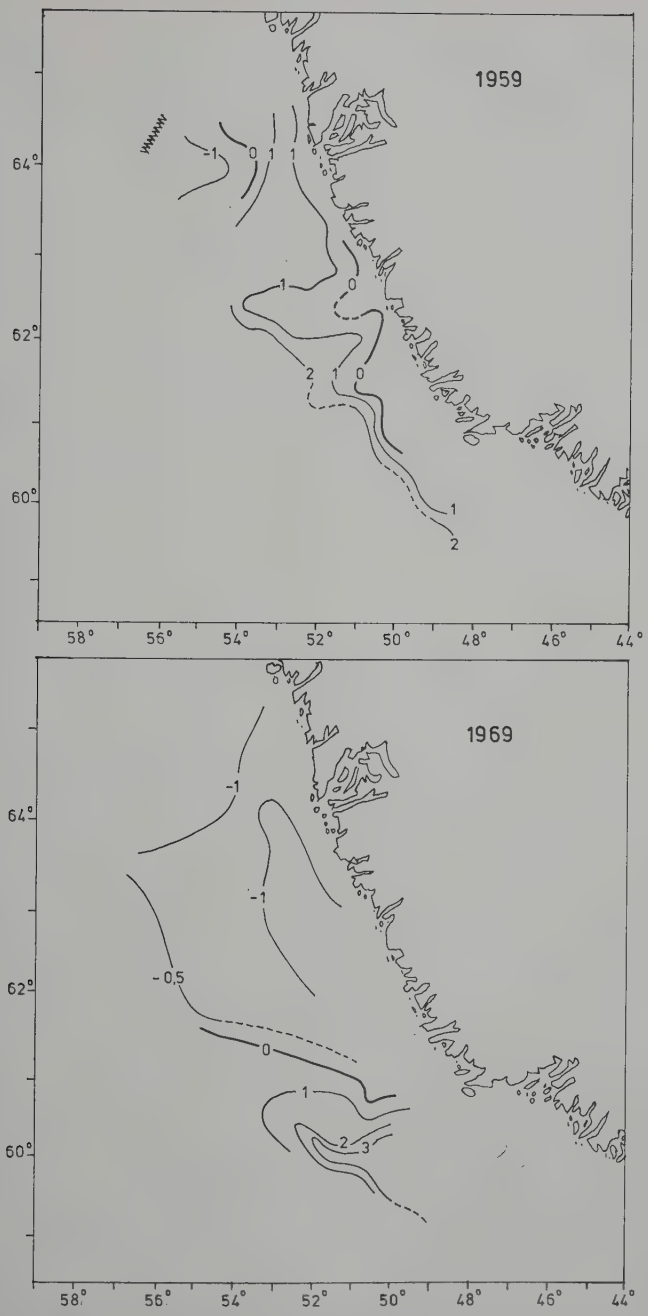

Fig. 2. Surface temperature as observed in April 1959 (top) and April 1969 (bottom).

RESULTS AND DISCUSSIONS

Fig. 2 shows the distribution of the surface temperature as observed in April 1959 and in 1969. Even though the chart for 1969 is lacking somewhat in detail, it is evident that the temperatures in the surface layer have decreased considerably during the period. In 1959 only a minor area close to the coast exhibited temperatures below 0°C while in 1969 the isotherm for 0°C was situated far from the coast, and the greater part of the survey area had sub-zero temperatures in the upper layers. By comparing similar charts for all years during the period it is seen that from 1961 the lateral extent of the Arctic Component of the West Greenland Current has increased gradually.

Sections across the Fylla Bank from 1961 and 1969 are shown in Fig. 3 and Fig. 4 respectively. They demonstrate the situation typical for the beginning and the end of the period. The increased lateral extent of the waters of Arctic and coastal origin in the West Greenland Current towards the end of the period is clearly seen. In the section from 1961 only the waters close to the coast was colder than +1°C with associated salinities about 34.1‰. In 1969 the temperature was below 0°C in the upper 52 m along the whole section, and the associated salinities had

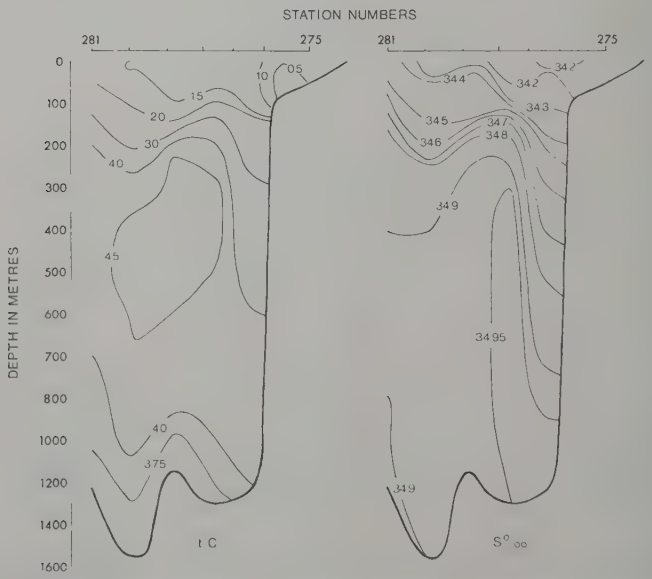

Fig. 3. Temperatures and salinities in a section across the Fylla Bank in April 1961.

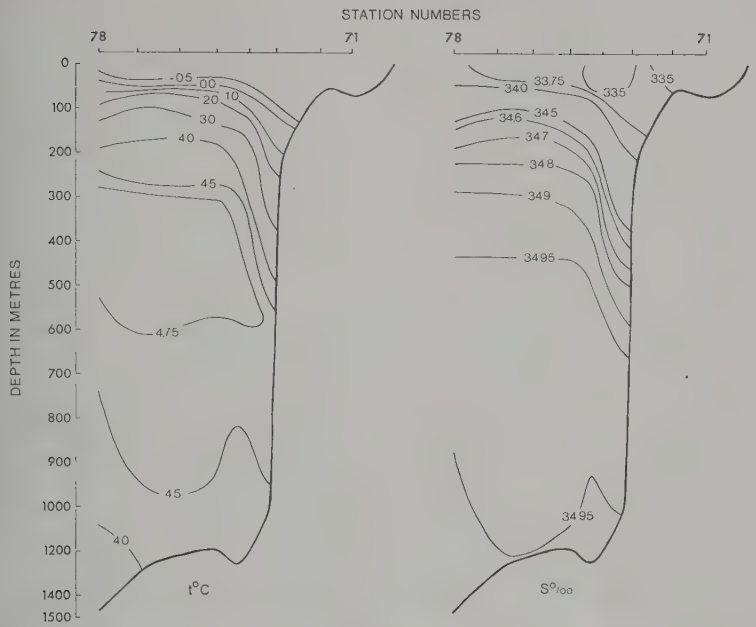

Fig. 4. Temperatures and salinities in a section across the Fylla Bank in April 1960.

decreased to between 33.5 and 33.8‰. The temperature decrease in the upper layers during the 11 year period is demonstrated by the curves in Fig. 5. The figure shows three years moving average of mean temperature and salinity in the Arctic Component of the West Greenland Current, i.e. in waters of salinity below 34.0‰. The figure shows that the temperatures have fallen gradually during the period and the difference between the mean for 1959 — 61 and 1967 — 69 amounts to 1.6°C. In the same manner the curve for the salinity shows a decrease of about 0.3‰, but during the last years of the period it shows a minor increase.

The Irminger Component of the West Greenland Current is seen in Fig. 3 and 4 as a temperature maximum at depths between about 300 and 600 m. It is shown in the figures that this water mass exhibited somewhat lower temperatures in 1961 than in 1969, the maximum being about 4.6 in 1961 and between 4.9 and 5.0°C in the end of the period. Fig. 6 which shows mean temperatures between 300 and 500 m depth in the Fylla sections, demonstrates the temperature trend in the Irminger Component more in detail. The mean feature demonstrated is a relatively cold period in the years 1961, 62 and 63 followed by an increase which culminated in 1966 when the mean temperature was 1.4°C

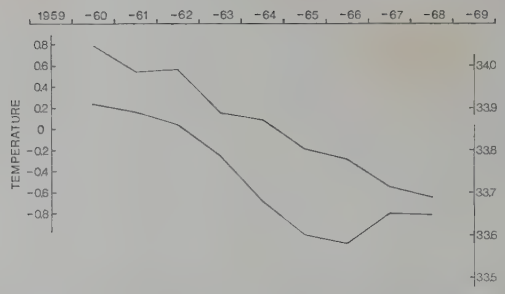

Fig. 5. Three years moving averages of temperature and salinity in waters of salinity below 34‰ in the section across the Fylla Bank.

above the mean value for 1963. During the following years the temperature decreased again to values below the overall mean for the 11 year period. A similar trend has also been observed in the other sections to the north and south of the Fylla Bank. The temperature increase until 1966 is in agreement with the trend in the July temperature which is reported on by HERMANN (1967).

A trend which is closely related to the trend in the Irminger water off West Greenland is also observed in the surface layer at OWS ALFA in the Irminger Sea as described by RODEWALD (1971). The fluctuations observed in the Irminger water of the West Greenland Current are, therefore, related to the conditions in the Irminger Sea. The reason is, as explained by RODEWALD (1971), the distribution of the atmospheric pressure and wind field which up to the mid 1960s were in favour of greate transport than normal of Atlantic water to the Irminger Current. At the same time, however, the supply of Arctic water to the East-, and consequently to the West Greenland Current was also enlarged and contributed to its increased offshore extent in the surface layer.

The decreasing salinity in the surface layer brought about a decline

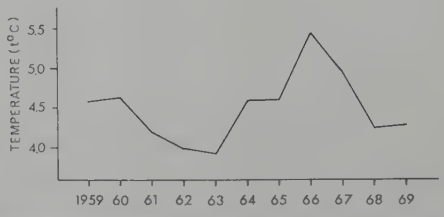

Fig. 6. Mean temperature between 300 and 500 m depth in the section across the Fylla Bank.

in density, the lowest values being observed in 1966, but densities remained low also during the rest of the period. In 1966 the mean δ_t-value in the upper 50 m of the Fylla section was 0.5 less than the value for 1960. Consequently the transition layer between the more or less Arctic waters of the surface layer and the Irminger water below became more pronounced, and the vertical exchange of heat by convection was consideraly reduced. During the winter season this resulted in an additional cooling of the surface layer because of radiant heat loss and only moderate heat supply from below. This seems also to be the reason for rising maximum temperatures in the Irminger Component from south to north. In the section across the Lille Hellefiske Bank the average maximum temperature in the Irminger water during the period was 5.11°C. This is respectively 0.22°C and 0.48°C higher than the associated averages in the sections across the Fylla and Dana Banks further south. A similar, but not so pronounced trend was also established for the salinity. This northward augmented preservation of the Irminger characteristics may be explained by a northward decrease in vertical convection during the winter season.

The vertical distribution of the temperature and salinity fluctuation is illustrated in Fig. 7. This figure shows a mean difference between the

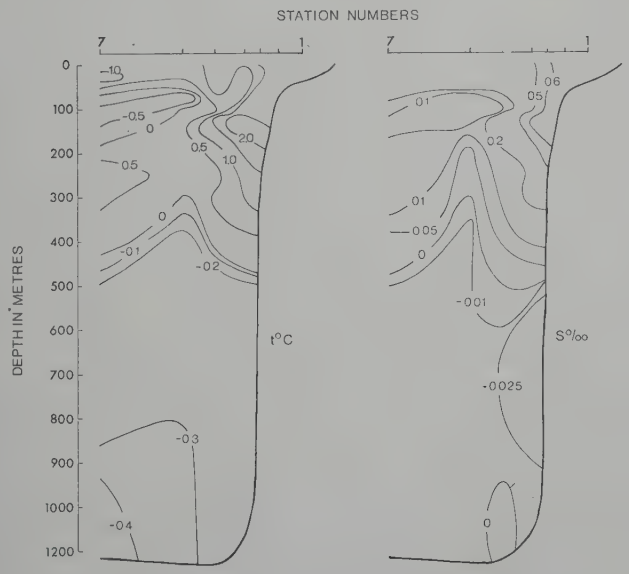

Fig. 7. Vertical distribution of differences in temperature and salinity between means for 1968—69 and 1959—61 in the section across the Fylla Bank.

beginning and the end of the period in the section across the Fylla Bank. It is based on the sections worked in 1959, 1961, 1968 and 1969. The temperature differences, t, which are depicted in the section are

$$t = \tfrac{1}{2}(t_{1968} + t_{1969}) - \tfrac{1}{2}(t_{1959} + t_{1961}),$$

and the salinity values are worked out in the same manner. The figure indicates that the temperature has increased down to about 400 m depth, the cooling effect being most pronounced over the shelf and slope. At 150 m depth just off the edge of the shelf the difference exceeded 2.0°C, the associated difference in salinity being between 0.6 and 0.7‰. The extent of Arctic water which spread out in the upper layers during the period, is indicated by a difference of about 0.5°C and 0.2‰ above approximately 50 m depth.

In 1968 and 1969 the transport of Irminger water to the Labrador Sea was diminishing compared to the inflow in the middle of the period as indicated in Fig. 6, but still it's temperature was higher in the beginning of the period. This is shown in Fig. 7 by the core which is indicated by rising temperatures at intermediate depths. It is also seen that the effect of the Irminger water, being mixed with surrounding water masses, can be traced down to depths of 1 000 to 1 200 m.

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ECOLOGICAL INVESTIGATIONS ON THE SPAWNING GROUNDS OF THE BARENTS SEA CAPELIN

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ABSTRACT

Sætre, R. and Gjøsæter, J. 1975. Ecological investigations on the spawning grounds of the Barents Sea capelin. *FiskDir. Skr. Ser. HavUnders.*, *16*: 203—000.

A programme to study the reproduction of the Barents Sea capelin was conducted by the Institute of Marine Research in Bergen during the period 1971 –1974. The present paper deals with the investigations on the spawning grounds along the coast of northern Norway.

During the years of investigations the spawning started between 1 and 15 March, and there was a gradual movement of the spawning area towards north and east during the observation period. The temperature during the incubation has been 1.5 and 6.5° C. The main spawning depth appears to be between 25 and 75 m. The extremes of the spawning depth observed was 12 and 280 m.

The capelin seem to prefer rather coarse substratum as gravel or cobble for spawning. The capelin eggs are mixed with the substratum to a layer up to 15 cm thick. This burying of the eggs is caused by strong current resulting in a sediment transport along the bottom.

Both diving ducks and haddock have been observed feeding on capelin eggs. This predations is probably of little importance although the haddock may consume significant egg quantities on some of the deepest spawning grounds.

INTRODUCTION

The Barents Sea capelin ,*Mallotus villosus*, is one of the most important resources for the Norwegian fisheries. The catch was reaching a peak, 1.6 mill. tons, in 1972. The main fishery is based on the spawning stock approaching the coast of northern Norway and Murman during February —April. The spawning stock is dominated by one or two yearclasses and wide flutuations in the spawning stock size may therefore be expected. Most of the capelin probably die after the spawning. There is also a spawning during summer and autumn but this seems bo be of minor importance and very little data is available (Prokhorov 1965).

Capelin has a circumpolar distribution and can be found in the northern regions of the Atlantic and the Pacific. The eggs are demersal

and stick to the bottom substratum. For spawning its preference with regard to depth, temperature and substratum seem to vary geographically, and the published accounts appear to be partly contradictory. Egg development takes 40—50 days at a temperature of 2.8 °C and 30 days at 5 °C (Pitt 1958, Pozdnjakov 1960).

A programme to study the reproduction of capelin was initiated by the Institute of Marine Research in 1971. This programme aimed to give a better understanding of the reproduction biology of capelin and to give data for the management of the fishery. It includes studies on the spawning influx, on the spawning grounds and on the larval drift.

Results from these studies have partly been published by Bjørke, Gjøsæter and Sætre (1972), Gjøsæter and Sætre (1973), Dragesund, Gjøsæter and Monstad (1973) and Gjøsæter, Hansen, Sætre and Westergaard (1974). Some diving observations from the spawning grounds were presented by Bakke and Bjørke (1973) and observations on predation of capelin eggs by eiders by Gjøsæter and Sætre (1975). A method for estimating the spawning stock size based on egg and larval data, and the application of this method on the Barents Sea capelin was described by Gjøsæter and Sætre (1974).

The present paper sums up the results from the spawning grounds investigations.

BEHAVIOUR

The behaviour of capelin on the spawning grounds was observed by SCUBA divers and by using echo sounders. Echo recordings indicate tha the capelin approach the spawning grounds in dense, pelagic schools (Fig. 1). These schools may contain several hundred tons. Sampling has indicated that males and females often form separate schools. As the schools reach the spawning ground, they may be recorded as settled on the bottom (Fig. 2) or as a continous layer along the bottom as seen on the left side of Fig. 3. This is a typical spawning layer. A Petersen grab with a 0.1 m^2 opening caught 30 spawning capelin from such a layer. At the right side of Fig. 3 spent capelin are leaving the spawning bed.

Excluding the pelagic migratory schools, the divers observed two types of schools at the spawning grounds. The first stype consisted of more or less regularly oriented capelin swimming forward or in circles (Fig. 4). The distance between the capelin was usually between 15 and 30 cm, and the size of the schools was highly variable. The schools

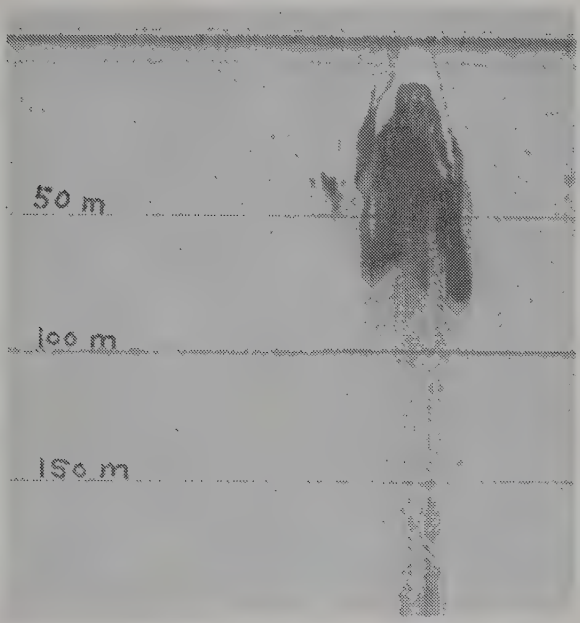

Fig. 1. Pelagic migration school of capelin.

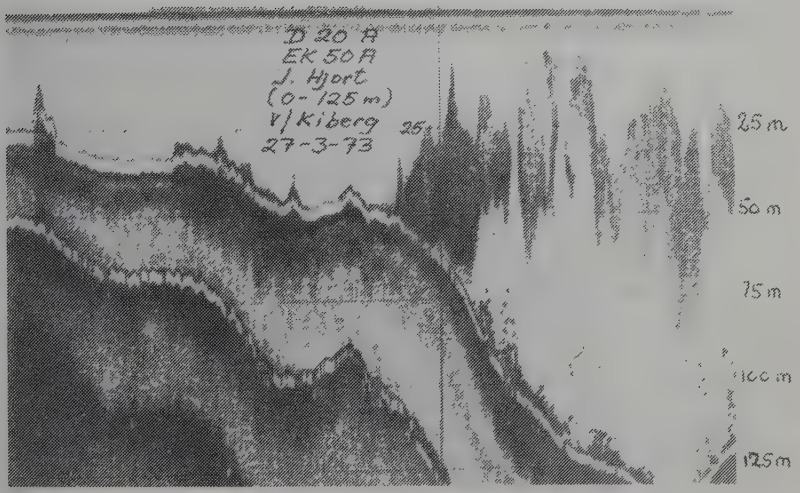

Fig. 2. Schools of capelin settling on the bottom.

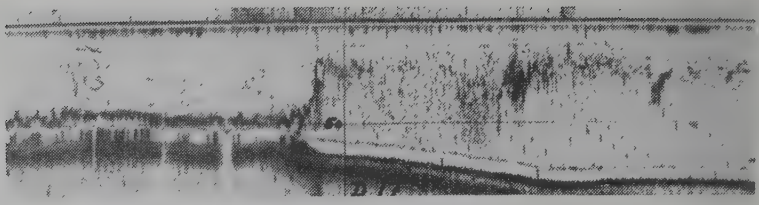

Fig. 3. Spawning capelin forming a layer along the bottom.

reacted collectively to stimuli, and they seemed to be attracted by white and shining objects. As two schools met, the capelin swam upwards in a disorderly manner but they soon gathered in separate schools again.

The second type of schools or masses was often pyramidal and consisted of irregularly oriented fish (Fig. 5). The lower part, having a diameter of about 3—5 m, was close to the bottom. The mean distance between the fishes was only 5 cm, and occasionally they were more concentrated. The activity was highest in the centre of the school.

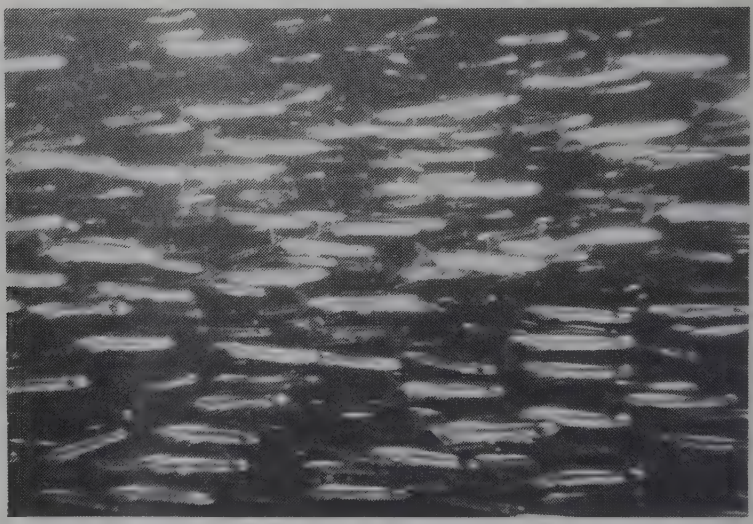

Fig. 4. School of regularly oriented capelin at the spawning ground.

Sometimes capelin from these schools were observed feeding on eggs whirled up from the bottom. Prespawning and spawning males were totally dominant in both types of schools, and females were seldom observed at the spawning grounds.

The spawning act was never observed, possibly because it mainly takes place during the night. The spawning has, however, been described for Canadian beach spawners (e.g. Sleggs 1933). Male capelin, which had finished spawning, were occasionally observed on the spawning grounds. They seemed to be in a very bad condition. Many of these, and also the dead males found on the bottom, had a permanent deflection on the side. This malformation probably appears during the spawning act when only one male spawns with a female and has therefore to take up a strongly curved position. Spent females were very seldom observed at the spawning grounds.

The two types of schools described here probably correspond with those described by Sleggs (1933) and Bakke and Bjørke (1973). Our observations indicate great variations in the swimming speed of the first type of school. These schools can probably search wide areas to find suitable spawning beds. Both our observations and those of Bakke and Bjørke (1973) agree that the schools reacted collectively to stimuli.

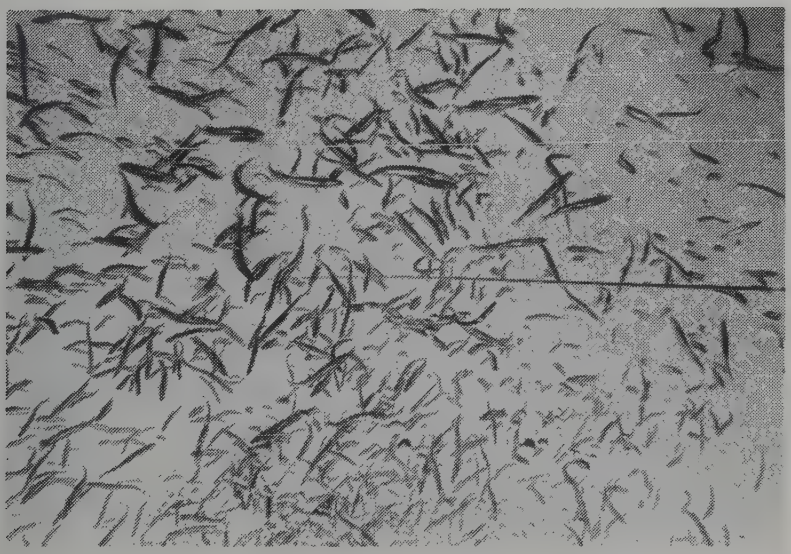

Fig. 5. Pyramidal school with irregularly oriented capelin.

The second type, described as «globular masses» by Sleggs (1933) and as «very dense formations» by Bakke and Bjørke (1973), most likely represent the last stage before spawning. These schools appeared to be rather stationary. They reacted only slightly to the presence of divers, and this reaction was individual and not common for the whole school.

LOCATION AND TIME OF THE SPAWNING

The spawning grounds were located by a combination of the following methods:

A) Monitoring the migration of the maturing capelin by echo surveys.
B) Following the development of the fishery and reports from the fishermen.
C) Analysing the stomach contents of demersal fishes (e.g. haddock).
D) Recording concentrations of diving ducks.
E) Sampling with a 0.1 m^2 Petersens grab.
F) SCUBA diving.

Methods A to D were used for limitation of the most likely spawning areas and methods E and F for confirmation and detail surveying. To confirm that alle the important spawning grounds had been found, the data from the larval surveys (Gjøsæter and Sætre, unpublished) were consulted.

Eggs, naturally spawned and artificially fertilized, were placed onboard in incubators for hatching at different temperatures. The results obtained, made it possible to calculate the age of the eggs (Gjøsæter, unpublished). Based on this, the time of spawning was estimated.

Fig. 6 shows the observed spawning grounds during the period 1971—1974. In 1971 the larval distribution indicates that some spawning also occurred farther south. This year concentrations of capelin were located as far south as Vesterålen which is the most southerly area of capelin catches during the last two decades (Dragesund *et al.* 1973). For the remaining years all major spawning localities are assumed to be included. These are always situated at the outer part of the coast.

There seems to be a gradual movement of the spawning area towards north and east during the observation period. Except for the years 1938—1942 and 1962 the capelin has been an unfailing guest along the coast of northern Norway for at least the last hundred years (Møller og Olsen 1962, Olsen 1968). The Vardø—Kiberg area seems to be the most regular spawning locality. Spawning west and south of Loppa is considerably less frequent.

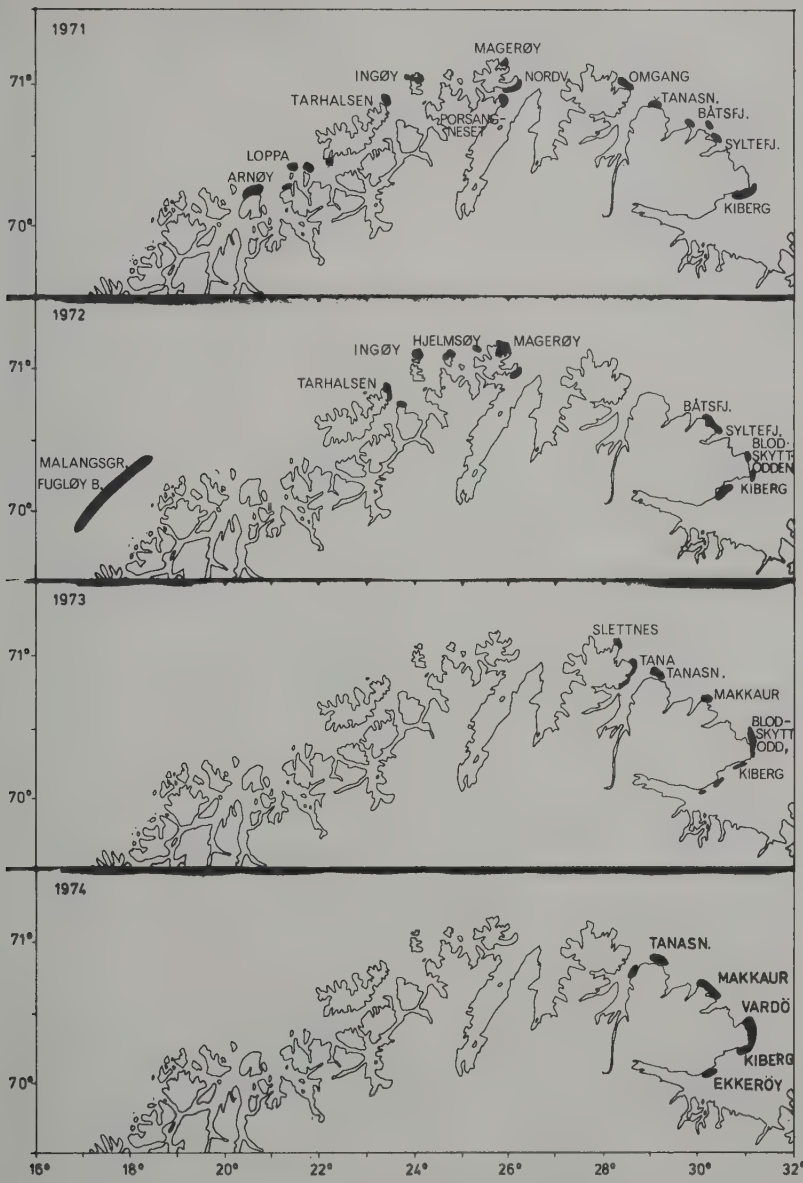

Fig. 6. Location of the observed spawning grounds.

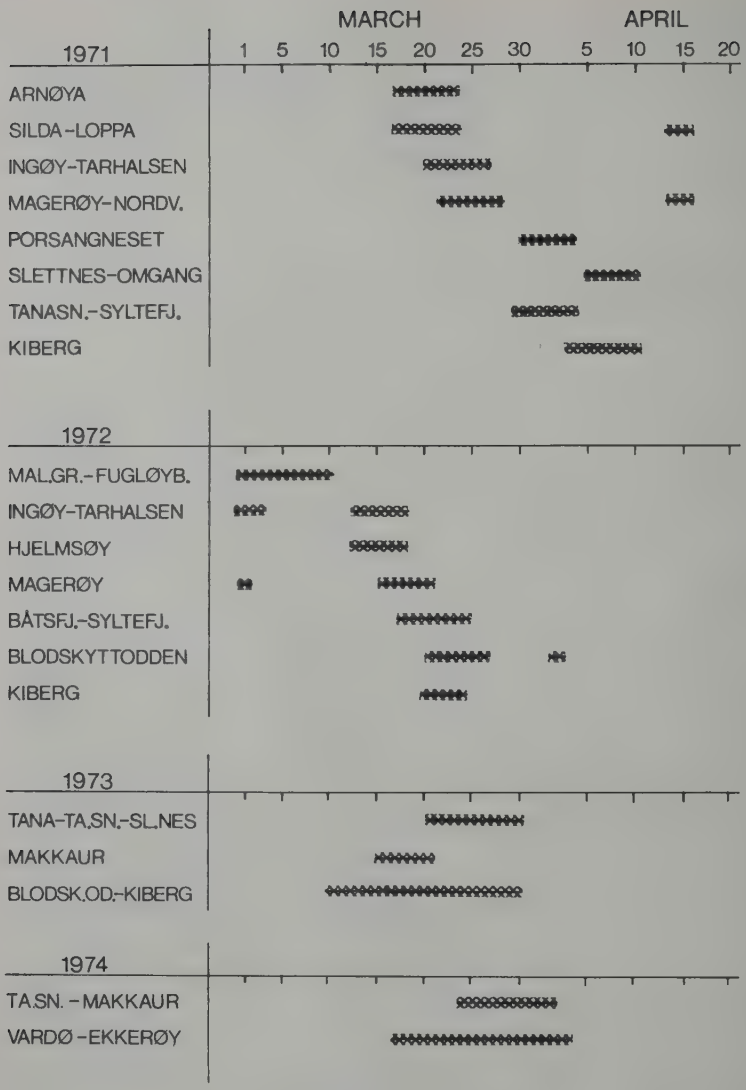

Fig. 7. Time and duration of the spawning.

Fig. 7 shows the time and duration of the spawning for the years 1971—1974. Usually there are several separate spawning runs at the different localities. The year 1971 appears to be somewhat anomalous in that respect. Mature capelin approached the coast in the Ingøy—Magerøy area continuously during February and March and proceeded farther west and south along the coast. (Dragesund *et al.* 1973). This may be due to spawning stock size which in 1971 was at a very high level. In the eastern part of the spawning area at Vardø—Kiberg only small concentrations of capelin were recorded. The spawning started in the southernmost area in the middle of March.

In 1972 two separate influxes occurred. The westernmost influx approached the coast in the Ingøy—Magerøy area from the north at the end of January. The capelin moved south and west along a route approximately 20 nautical miles from the coast (Blindheim og Monstad 1972). The spawning started at the Fugløybank and Malangsgrunnen in the beginning of March. In the middle of March a second influx reached the surroundings of Vardø. This part of the spawning stock moved westward.

In 1973 the capelin influx followed the coast of Murman and reached Vardø at the end of February (Jacobsen og Nakken 1973). The spawning started in this area about 10 March.

Three independent spawning runs were present in 1974. The first one approached Omgang from the north and turned eastwards along the coast. The second influx reached Vardø from the northeast, and the third followed the coast of Murman towards Kiberg (Anon. 1974). The spawning started in the Vardø—Kiberg area about 15 March.

During the last century the first spawning run has reached the Norwegian coast between the beginning of February and the end of April. An early arrival of the capelin appears to be associated with a westerly distribution (Olsen 1968, Gjøsæter 1972).

HYDROGRAPHIC CONDITIONS

The bottom temperature and salinity were measured throughout the whole incubation time. Current measurements with recording instruments of the Aanderaa type were carried out close to the sea floor at several spawning beds.

Table 1 shows the hydrographic conditions during the spawning seasons 1971—1974. The lowest temperature during the time of incubation was recorded in 1971 when the capelin started to spawn in water of 1.5°C. The high upper limit in 1972 is due to the spawning in more oceanic water masses at the Malangsgrunnen and the Fugløybank. The salinity

Table 1. Hydrographic conditions during the spawning seasons 1971—1974.

Year	t °C during incubation	S ‰ during incubation	t_{100} Ingøy	S_{100} Ingøy	Temperature anomaly	
					Loppa	Vardø
1971.....	1.5°—3.5°	34.1—34.4	3.72°	34.470	—1.0°	—0.9°
1972.....	2.5°—6.5°	34.1—34.6	4.85°	34.560	+0.5°	+0.7°
1973.....	2.0°—4.0°	34.4—34.6	4.82°	34.658	+0.8°	+0.9°
1974.....	2.5°—4.0°	34.4—34.6	4.59°	34.651	+0.2°	+0.6°

at the spawning beds during the period 1971—1974 has been between 34.1 and 34.6‰ which is about the normal salinity for the coastal waters along northern Norway.

Table 1 also shows the mean temperature and salinity for the upper 100 m at a fixed oceanographic station off Ingøy during March—April and the temperature deviations from the normal 1936—1970 for the surface layer at Loppa and at Vardø (Sætre 1973). It is quite obvious that 1971 is characterized by a small influence of Atlantic water masses along the coast of northern Norway and 1973 as the year of the most marked Atlantic influence.

Previous observations of the spawning temperature of the Barents Sea capelin are rather few. Rass (1933) reports spawning in about 2 °C, and Olsen (1968) observed spawning in temperature between 2.5 and 5 °C. Listed in Table 2 are spawning temperatures of capelin reported from other areas. It appears that the temperatures at Greenland and on the Grand Banks are very similar to those observed by the present authors.

Table 2. Temperatures in some capelin spawning areas.

Area	Spawning temperature	Author
Newfoundland, beachspawners.	5.6°—10.0°	Sleggs 1933, Templeman 1948
Newfoundland, Grand Banks .	2.8°—4.2°	Pitt 1958
British Columbia	10.0°—11.0°	Hart and McHugh 1944
Iceland.....	6.0°—7.0°	Jespersen 1920, Magnusson 1966
Greenland	1.9°—6.6°	Kanneworff 1968

FLORA AND FAUNA ON THE SPAWNING GROUNDS

The macro flora on the spawning beds included some dispersed *Laminaria digitata*. Various corallinaceae and other red algae were also found. Some eggs were overgrown with small filamentous colonies of diatomea. This occurred only at depths between 10 and 30 m and only

Table 3. Some animals from the spawning grounds.

Phylum	
Porifera	Various species
Cnidaria	Various thecaphore hydroida
Plathyhelmintes.	Turbellaria
Nemertini.....	Various species
Aschelminthes .	Various nonparasitic nematoda
Arthropoda	Ostracoda
	Copepoda, mainly harpacticoida
	Cirripedia
	Cumacea
	Amphipoda
	Mycidacea
	Decapoda, e.g. *Hyas, Pagurus.*
Mollusca	Polyplacophora
	Gastropoda
	Bivalvia, e.g. *Cyprina, Clamys, Modiolus*
Annelida	Polychaeta
Ectoprocta	Many species
Brachiopoda ...	Various species
Echinodermata .	Asteroidea, e.g. *Asterias*
	Ophiueoidea
	Echinoidea, e.g. *Strongylocentrotus, Spataugus*
	Holothuroidea
Chordata	Pisces: *Gadus morhua, Melanogrammus aeglefinus, Pollachius virens, Ammodytes sp. Anarhichas lupus, Pleuronectes platessa.*

on eggs lying on the top of the substratum. Laboratory experiments suggested that these algae had no noticeable effect on the development of the eggs.

The fauna on the spawning grounds was usually sparse and the total biomass very low. No systematic collection was carried out, but some taxa, commonly observed in grab samples or by divers, are listed in Table 3. None of the invertebrates seemed to feed noticeably on eggs or significantly alternate their environment.

DEPTH AND SUBSTRATUM OF THE SPAWNING

After the location of the spawning grounds, some of the spawning beds were selected for a more detailed investigation. A Decca map in the scale of 1:5000 or 1:10000 was constructed covering the selected spawning bed. The Decca Navigator System has a high resolution in coastal waters and thus make it possible to navigate with a high relative accuracy. A detailed surveying of the spawning bed was performed using grab and SCUBA divers. The divers were equipped with sampling tubes

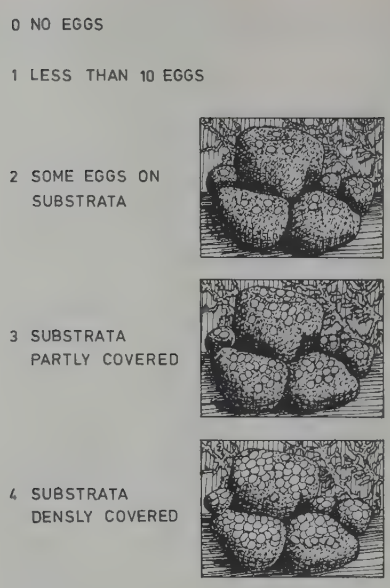

Fig. 8. Scale for classification of egg quantity.

which enabled them to take samples where the stratification of the bottom substratum was undisturbed. The divers also filmed and photographed on the spawning beds.

The amount of eggs in the grab samples were subjectively classified from 0 to 4 according to the scale shown in Fig. 8. No eggs in the sample were denoted 0 and the highest densities of eggs designated 4. The decisive factor for the classification was the ratio between number of eggs and the quantity of bottom substratum in the sample. The order of size of the egg densities corresponding to the different egg quantities appears in Table 4.

Table 4. Corresponding values of egg quantities and egg densities.

Egg quantity	Egg density eggs/m²
0	None
1	10^1—10^3
2	10^3—10^5
3	10^5—10^6
4	10^6—10^7

The size distribution of the sediment agregates was classified according to the Wentworth scale (WENTWORTH 1922). This scale is a geometrical one using the particle diameter in mm raised to the powers of 2 as steps between successive elements of the series. KRUMBEIN (1936) used the exponents, that is, the powers of 2 in the Wentworth series as the basis for a logarithmic scale of sediment size. He defined a unit, Φ, as the negative logarithm to the base of 2 of the particle diameter in millimeters, $\Phi = -\log_2 D$. The logarithmical scale is chosen as most of the physical properities of a sediment are found to vary as some power of sediment size rather than directly with size.

Table 5. Depth distribution of egg quantity 0—4 in grab samples 1971—1974.

Depth in m	Egg quantity					Sum
	0	1	2	3	4	
0— 24	221	83	32	16	15	367
25— 49	820	171	100	52	33	1 176
50— 74	387	69	31	5	5	497
75— 99	170	16	9	4	1	200
100—124	78	5			1	84
125—149	51	2	1			54
150—174	23	3				26
175—199	22	1				23
200—224	6	1	1			8
225—249	2		1			3
250—350	9	1				10
Sum	1 789	352	175	77	55	2 448

Table 5 shows the distribution of egg quantities 0—4 at different depths for all the grab samples during the period 1971—1974. Fewer high egg densities are found (i.e. egg quantity 3 and 4) as the depth of the grab samples is increased. In 0—24 m 8.4% of the samples contained egg quantity 3 or 4, in 25—49 m 7.2% and in 50—74 m about 2%. The most shallow spawning bed observed is Nordvågen in 1971 with depths between 12 and 18 m. The deepest sample containing capelin eggs is from 280 m off Vardø in 1973. The samples from the deeper parts are few and the probability of getting a correct sample will decrease with increasing sampling depth. Although the sampling design makes the data unsuitable for statistical treatment they still indicate that the main spawning take place in the upper 75 m.

Information concerning the depth of spawning of the Barents Sea capelin is rather divergent. The suggestions that appear to be in best accordance with our observations are those by RASS (1933) (50- 100m) and MOLLER and OLSEN (1962) (10—100 m

Along the coast of Newfoundland and Labrador the beach spawning is often succeeded by spawning at increasing depth down to at least 55 m (Templeman 1948). Pitt (1958) reported indications of spawning on the Grand Banks at depths between 46 and 80 m.

The capelin eggs observed by us in the deepest samples may have been spawned at this depth or they may have been transported there from shallower spawning beds. Bottom trawl used at about 250 m depth several times caught haddock with a stomach content of recently swallowed fertilized capelin eggs. This supports the first explanation. Though the main spawning occurs in the upper 100 m, the Barents Sea capelin seems to be able to spawn down to at least 250 m.

Table 6. Distribution of egg quantity 0—4 at different substrata in grab samples 1971—1974.

Substrata	Egg quantity					Sum
	0	1	2	3	4	
Pebble-gravel	129	39	29	19	27	243
Shell gravel	387	71	55	29	15	557
Hard bottom-cobble ...	1 036	192	62	23	12	1 325
Mineral sand	144	47	27	6	1	225
Silt-Clay	93	3	2			98
Sum	1 789	352	175	77	55	2 448

In Table 6 is listed the distribution of egg quantities 0—4 at different substrata. The table shows that gravel or pebbles is the most preferred substratum for spawning. About 19% of the samples from this bottom material contained egg quantity 3 or 4. Shell gravel also occurs as a spawning substratum. About 8% of these samples were classified as egg quantity 3 or 4. At hard bottom and mineral sand between 2.5% and 3% of the grab samples contained egg quantity 3 or 4. Eggs were rarely observed on silt and clay.

Fig. 9 shows a typical size distribution of pebble substratum at Blodskyttodden. The size frequency distribution is represented by a cumulative percent curve of weight. The median Md, which is the diameter size at 50% of the cumulative frequency curve, amounts to 8.25 mm. Trask (1932) defined a sorting coefficient as $S = \sqrt{\frac{Q_3}{Q_1}}$ where Q_1 and Q_3 are the diameter in millimeters dorresponding to the 25th and 75th percentiles, respectively, of the cumulative curve. S in the distribution shown in Fig. 9 is 1.55 which indicates a well sorted sediment.

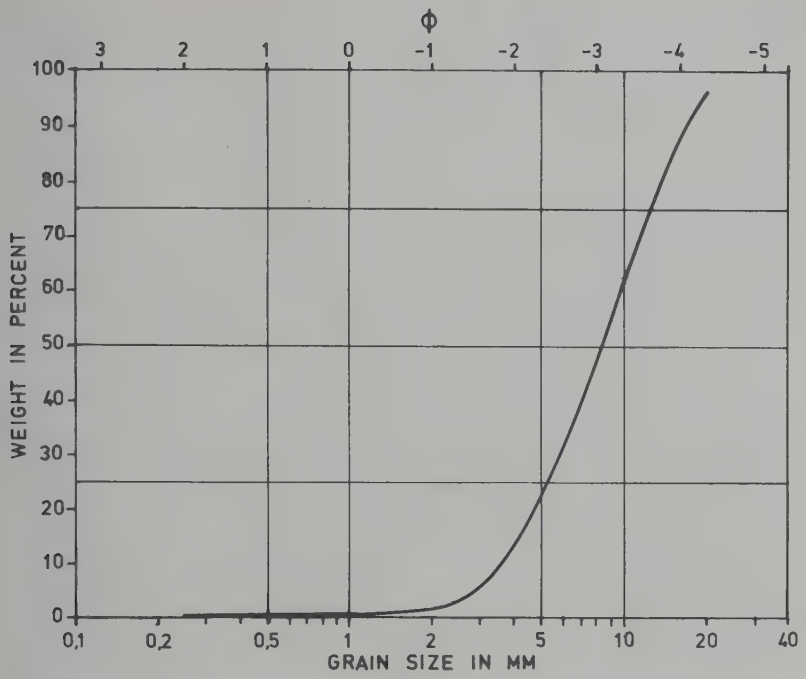

Fig. 9. Typical grain size distribution of pebble substratum from a spawning bed. For explanation see text.

The median of the pebble or gravel substratum where spawning occurred varied between 5 and 15 mm and the sorting coefficient between 1.3 and 1.6. On cobble spawning was observed on substratum up to a size of 60 mm in diameter.

The capelin seem to prefer rather coarse material for spawning. Sleggs (1933) states that the Newfoundland beach spawning capelin prefer to spawn on gravel beach. Templeman (1948) confirms this and observed a grain size from 2.5 to 15 mm to be especially favourable for spawning. For the deeper spawning grounds Pitt (1958) reports spawning at a grain size from 0.5 to 2.2 mm at Grand Bank. Prokhorov (1965) also believes the spawning of the Barents Sea capelin to take place on sandy grounds with shell fragments. The observations of the last two authors are based on recordings of the stomach content of haddock and capelin where swallowed substratum particles were found together with capelin eggs. It is not believed that this method shows representative measure of the grain size at the spawning beds. As shown in Fig. 9 the gravel or pebble substratum also contains particles belonging to the sand fraction. From our investigation it appears that the haddock selects

the eggs attached to the smallest particles (GJØSÆTER and SÆTRE, unpublished). We therefore question the statements of an offshore spawning on a sandy bottom. We have indeed observed high egg densities in grab samples consisting mainly of sand (Table 6). This seems to be due to patches of sand in a substratum of coarser materials.

DISTRIBUTION OF EGGS ON AND IN THE SUBSTRATUM

The methods used for these investigations are the same as those described in the section on depth and substratum of the spawning.

As indicated by Table 6, the preferred spawning substratum is gravel, pebble, shell gravel and cobble. Fig. 10 shows egg quantity 4 on gravel

Fig. 10. Eggs at gravel bottom (Egg quantity 4).

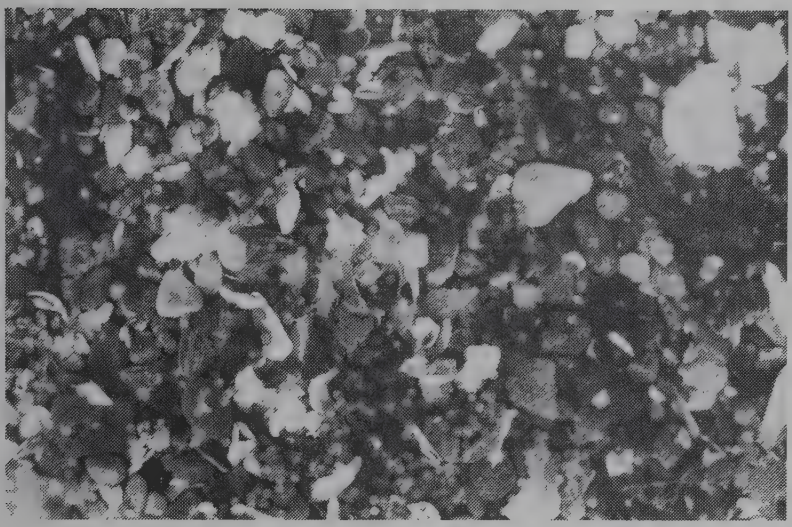

Fig. 11. Eggs at gravel bottom with shell fragments (Egg quantity 3).

bottom. A more detailed picture is shown in Fig. 11. Fig. 12 shows eggs on bottom consisting of shell gravel. A conspicuous feature of the egg distribution on these substrata is that the eggs are attached to the single particles. The layer of bottom substratum with eggs can reach a thickness of 15 cm, but 5—7 cm is the most usual.

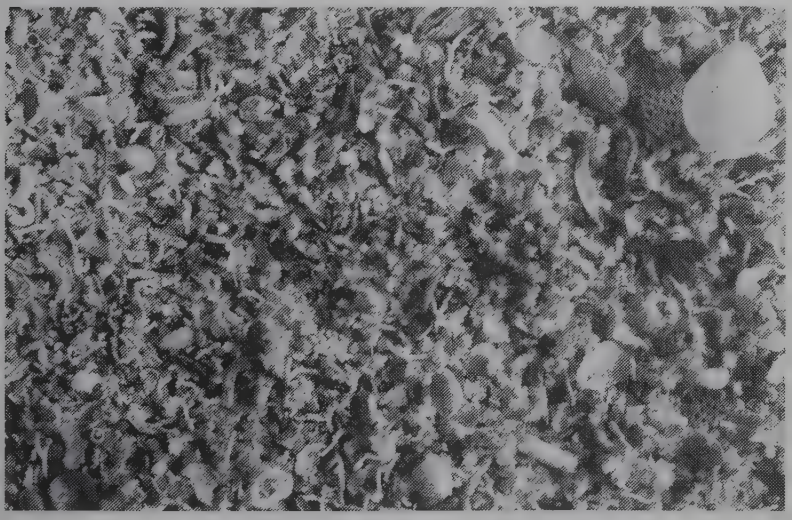

Fig. 12. Eggs at shell gravel.

Fig. 13. Layers of eggs at cobble.

On cobble the eggs are less mixed with the substratum and more attached to each other. Fig. 13 shows eggs on such a bottom together with empty shells. Fig. 14 gives a more detailed picture of the egg distribution. The egg layer of the cobble rarely exceeds 3 cm. The egg distribution is usually homogenous within a spawning bed. An abrupt change in egg density corresponds with a transition of the bottom substratum.

Fig. 14. Eggs and fauna from hard bottom.

The capelin eggs, found in gravel and shell gravel, are mixed with the substratum to a layer up to 15 cm thick. Although the capelin may be capable of doing some active burying, they certainly are not able to bury them to this depth. On most of the gravel and shell gravel spawnings beds the SCUBA divers observed periodic undulation in the bedding plane (Fig. 16). These so-called ripple marks are commonly observed in sand, but appear to be rather seldom in coarser materials (Allen 1968). The ripple marks observed had a wave length of 1.0—2.0 m and an amplitude of 0.2—0.5 m. According to the classification of Allen (1970) they are called dunes. The gravel dunes were longcrested and usually elongated transversely to the dominant current directions. The current is the generating force of these dunes, and they will move with the water flow. Due to erosion the material on the crests is coarser than in the troughs. The lighter material, such as eggs, is accumulated in the troughs which are therefore visual as light parts in Fig. 11. Along the coast of northern Norway there is a rather strong and alternating tidal current approximately parallel to the coast. The dunes thereby will move back and forth and thus mix the eggs into the substratum.

Though the mechanism governing the formations of ripples and dunes is still not fully understood, the appearance of these is evidence of sedimentary displacement along the bottom.

Fig. 16. Ripple marks on a gravel spawning bed.

The mean egg density at egg quantity 4 is calculated within 95% confidence limits to $4 \cdot 10^6 \pm 1 \cdot 10^6$ eggs/m². If a fecundity of 10^4 eggs (Gjøsæter and Monstad 1973) and a sex ratio of 1 : 1 are assumed, this will correspond to approximately 800 spawning capelin per square meter. The egg density expressed in eggs/cm³ substratum, will decrease with depth in the mixture of eggs and substratum. Typical examples of vertical distributions are shown in Fig. 15.

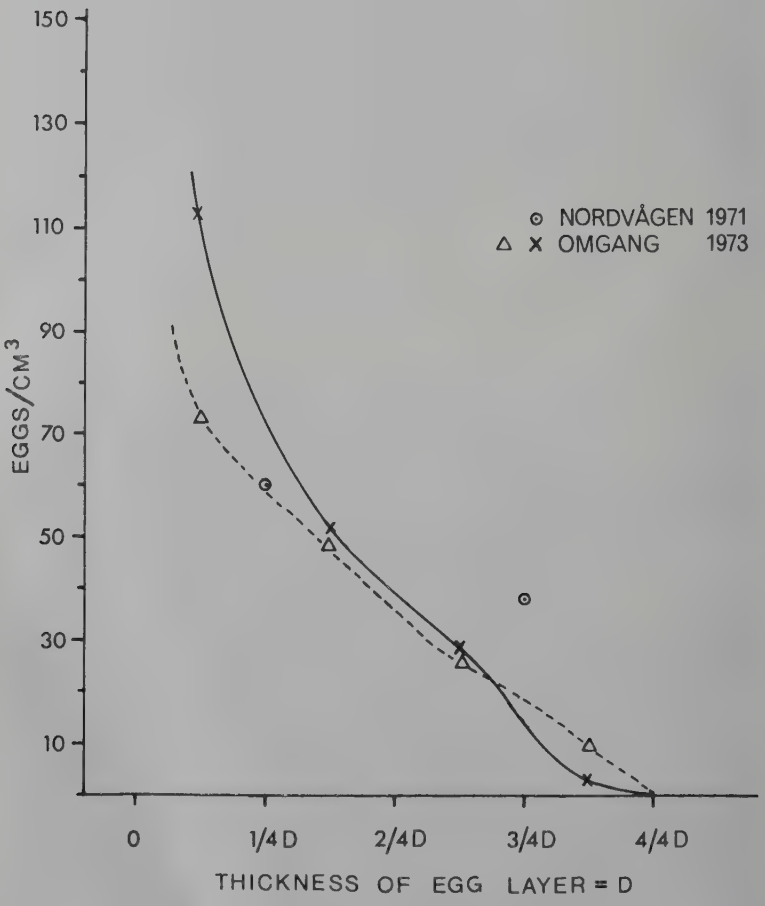

Fig. 15. Vertical distribution of eggs in the substratum.

Hjulstrøm (1939) has constructed a diagram to predict the critical conditions for the beginning of sediment movement as a function of current velocity. According to his diagram particles of size 5 mm are transported at a current of 40 cm/sec and particles of size 10 mm at 70 cm/sec. Current measurements on the spawning beds confirm that these values quite often are exceeded. It is obvious that the critical conditions for the commencement of the sediment transport cannot be deduced entirely from the grain size. The critical water velocity also varies with the excess density ($\varrho_s - \varrho$) of the grain where ϱ_s is the density of the solid grain and ϱ is the density of the water. Shell fragments therefore demand a lower velocity to move than pebbles of the same size. Eggs attached to the particles will reduce their density. This effect will increase with decreasing particle size. Therefore, to move a particle covered with eggs the strength of the current will be less than that deduced by the diagram of Hjulstrøm (1939), and this descrepancy will increase as the grain size is reduced.

The eggs of the Newfoundland beach spawning capelin are also mixed with the gravel. The thickness of this mixture can exceed 30 cm (Sleggs 1933). In this case it is the wave action which is the causal factor governing the burying.

At the spawning beds with egg layers thicker than approximately 5 cm there was a retardation in the development of the eggs from the deepest layers. This retardation became more pronounced during the incubation period. This is probably due to decreased availability of oxygen in the deepest layer. However, the viability did not appear to be influenced by this.

EGG MORTALITY

The reduction in number of eggs at the spawning grounds can be attributed to factors as rate of fertilization, drift of eggs and predation.

The rate of fertilization seems to be very close to 100% both in natural environment and in the laboratory. Outside the main spawning beds lower rates of fertilization were sometimes observed. Very little is known about the fate of the eggs that drift away from the spawning beds. Lillelund (1961) has, however, shown that eggs of the closely related *Osmerus eperlanus* usually survive although they drift freely in the water masses. Bakke and Bjørke (1973) observed a reduction in egg density on the surface of the substratum in Nordvågen in 1971, and they believed this to be due to drift of eggs. Later investigations indicate, however, that drift of eggs is usually of little significance, and the observed reduction

in egg density on the surface was probably due to the eggs being buried in the gravel.

Water from the fish pumps used onboard the fishing ships often contains large number of eggs. Samples from this water, which go back to the sea, contained fertilized eggs. These eggs had retained their ability to stick to other objects. Most of them survived till the experiment was concluded at the blastula stage.

Predation by fish is often the most significant cause of mortality in demersal eggs. The most important predator is haddock.

In 1971 spawning was mainly observed in shallow water (less than 80 m), and only an insignificant number of haddock and other fish were found at the spawning grounds.

In 1972 part of the spawning took place in deeper waters, and at spawning grounds deeper than 150 m haddock was abundant. Seventy percent of the haddock caught at Malangsgrunnen contained capelin eggs. The number of eggs in each stomach ranged between 5000 and 10 000. Saithe and cod were also observed on the spawning grounds, but they did not feed on eggs. In trawl catches in the Malangsgrunnen area there were more haddock compared to saithe and cod at stations where capelin eggs were found. The mean length of haddock was lower and the degree of filling of their stomachs higher at stations with eggs than at stations without. The material available is too sparse to decide whether the haddock, and especially the small haddock, concentrates at the spawning grounds.

In 1973 and 1974 predation by haddock was also recorded at the deeper spawning grounds, but the predation was less than in 1972. It is not possible to assess the quanta of capelin eggs consumed by haddock, but it may be a significant part of the eggs spawned in water deeper than 100—150 m.

Haddock feeding on capelin eggs have been observed both in the Barents Sea and in Canadian waters, and it is supposed to constitute an important part of the haddock's diet during the capelin spawning season (Zenkevitzh 1963, Templeman 1965). Templeman (1965) observed haddock feeding on capelin eggs at spawning beds lying as shallow as 40 m.

At spawning beds shallower than approximately 50 m flocks of ducks were observed feeding on capelin eggs. In 1972 the flocks consisted of about 3/4 king eiders (*Somateria spectabilis*) and 1/4 common eider (*Somateria mollissima*) and long-tailed duck (*Clangula hyemalis*).

In 1973 and 1974 king eiders were even more dominating and long-tailed ducks very sparse.

The ducks concentrated over the spawning beds as soon as the spawning started, and they disappeared during the hatching period. Although

the ducks were numerous, calculations indicate that the quanta of eggs consumed were less than 2—3% of the total egg production (Gjøsæter and Sætre 1975).

Common eiders have also been observed feeding on herring eggs (Soleim 1942, Cantin, Bedard and Milne 1974).

Capelin have often fertilized capelin eggs in the stomach, and in 1974 the divers saw capelin feeding on eggs. This predation is, however, probably of little importance.

Table 7. Mortality of capelin eggs at different egg quantities.

Mortality %	Egg quantity				Sum
	1	2	3	4	
<5%	10	19	14	13	55
5<10%	2	10	10	8	31
10<20%	7	3	4	1	15
20<50%	6	8	—	—	15
≥50%	12	2	3	—	17
Sum	37	43	32	21	133

The percentage of dead eggs was recorded in 132 samples from various parts of the spawning area (Table 7). In general the mortality was lowest where the egg density was highest. Even where the mixture of egg and gravel was as thick as 15 cm, no vertical gradient in mortality could be observed. Many of the eggs recorded as dead were mechanically destroyed. Parts of these eggs were probably destroyed by the sampling process.

Eggs which had completed approximately 2/3 of their developmental time (embryo with pigmented eyes and capable of strong movements), showed no increase in mechanical destruction, but slightly reduced viability when trawl bobbins were towed through the spawning beds (Bakke and Bjørke 1973, Dragesund *et al.* 1973).

Laboratory experiments (unpublished) also indicate that the eggs can endure fairly strong mechanical stress. The experiments indicate, however, that the susceptibility to mortality varies with the age. It seems to be high until the closure of the blasthophore, then it decreases, but it apparently increases again during the last period before hatching. Comparable development in the vitality has also been observed for other species (e.g. Riley 1974, Pommeranz 1974).

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INVESTIGATIONS ON DIEL VERTICAL MIGRATION OF 0—GROUP FISH IN THE BARENTS SEA

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ABSTRACT

Beltestad, A. K., Nakken, O. and Smedstad, O. M. 1975. Investigations on diel vertical migration of 0-group fish in the Barents Sea. *FiskDir.Skr.Ser.HavUnders.*, *16*: 000—000.

In August—September diel vertical migration of 0-group fish was studied in the Barents Sea. Redfish and capelin had different vertical migration patterns. 0-group redfish were found at the surface at dark and spread in the upper 50 m during the daylight period while the unpigmented 0-group capelin stayed in small schools close to the surface by daylight and dispersed into a weak scattering layer at the depth of the thermocline (20—30 m) at dark. This behaviour might introduce large errors to the abundance indices of 0-group capelin.

Comparative fishing with a pelagic trawl and a purse seine were carried out. The samples showed no significant differences in the length distributions of each species of 0-group fish caught with the two gears.

INTRODUCTION

During late summer and early autumn fish fry of many species occur pelagically in the Barents Sea. Since 1965 joint international surveys have been carried out annually in this area during 12—15 days in late August and early September. The primary aim of these surveys has been to map the geographical distribution and to obtain estimates of yearclass strength of the different species of 0-group fish. Preliminary results have each year been reported to the International Council for the Exploration of the Sea (Anon. 1965—1974 a).

The distribution and density of the pelagic layers of 0-group fish have been observed with echo sounders, echo integrators and small meshed pelagic trawls. Details of the technique applied are given in Dragesund, Midttun and Olsen (1970), and a thorough description and discussion of the method was made by Anon. (1974b).

The main results from these surveys are indices of yearclass strength (Haug and Nakken 1973). These indices might be influenced both by the sampling efficiency of the pelagic trawls and by the behaviour of the

fish. The vertical migration of the different species may thus effect observations both with echo sounders and pelagic trawls.

Diel vertical migration is a well known feature of the behaviour of most pelagic fishes. Woodhead (1966) and Blaxter (1970) have reviewed the literature on the subject. Normally, pelagic fishes are found at intermediate depths during the day, they move towards the surface at dusk and descend at dawn. This general pattern will probably vary with fish size, species and environmental factors. Although a few investigations have been carried out on redfish larvae (Kelly and Baker 1961 a, Kelly and Baker 1961 b, Magnusson, Magnusson and Hallgrimsson 1965), the diel vertical migration pattern of the 0-group fish in the Barents Sea was considered to be insufficiently known. During the survey in 1974 experimental work was therefore conducted to study this subject, and the results from the experiments are reported here.

MATERIAL AND METHODS

The investigations were carried out with the 600 tons purse seiner «Havdrøn» which is also fitted for pelagic trawling and equipped with Scientific sounder, EK 38, two echo integrators, QM, and a net sonde. Observations were collected in three different localities (Fig. 1). The periods of observations were as follows:

Area 1: 27—29 August Area 2: 1— 3 September
Area 3: 4— 5 September

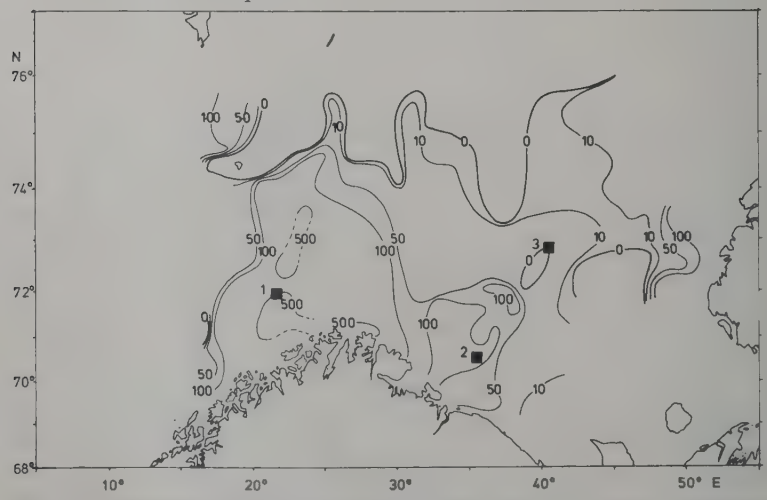

Fig. 1. Localities where diel vertical migration pattern of 0-group fish were studied in August—September 1974. 1) Area 1, 2) area 2, 3) area 3. Isolines indicate the echo integrator deflections observed during the international 0-group survey.

The selection of the areas were made on basis of information from the other vessels which participated in the survey. A standardized sampling procedure was followed in all three areas. An anchored bouy was used as a fixed position. Another bouy, attached to a free floating drogue in 25 m depth, was used as the point of reference for a small scale survey (Fig. 2). The grid of the small scale survey was continuously adjusted to keep the drogue at point A (Fig. 2). The arrows in Fig. 2 indicate «Havdrøn»s courses, and during one small scale survey the ship sailed 32 nautical miles. Between each completed survey one trawlhaul, one hydrographic station, one plankton haul and one series of light measurements were taken (Fig. 2). In each of the areas 1 and 2 ten small scale surveys were carried out while five completed surveys were found to give sufficient information in area 3.

When the weather conditions permitted, the 0-group fish scattering layer was observed by scuba divers. The divers observed the water column from 0 to 30 meters once by daylight and once at dark in area 2, and once at dark in area 3.

The four echo integrator channels were continuously monitoring the following depth intervals: 6—15 m, 15—30 m, 30—60 m, 60—200 m.

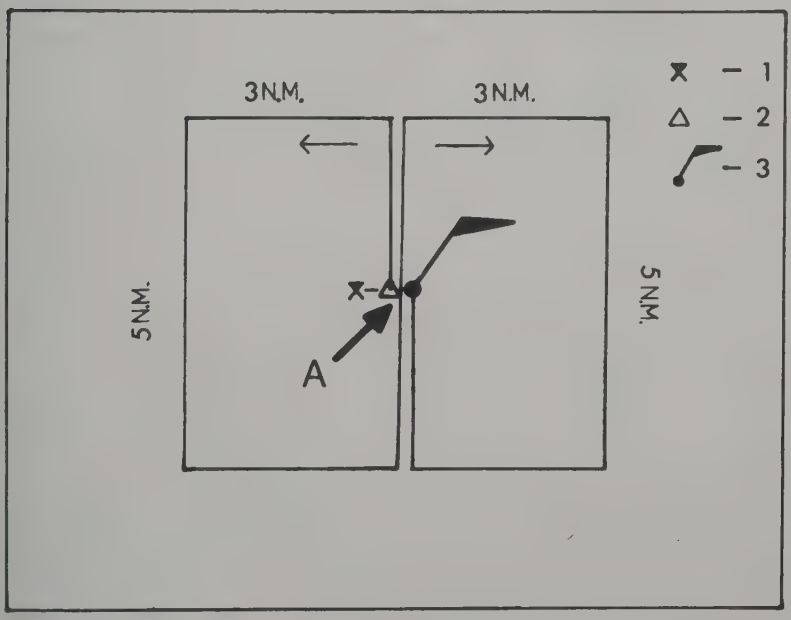

Fig. 2. The small scale survey conducted in the three areas. A) Start and end. 1) Hydrography and plankton station, 2) pelagic trawl and purse seine station, 3) drogue.

Their outputs were read for each nautical mile and then averaged for each half completed small scale survey. The values were converted to R.V. «G. O. Sars» values in order to be directly comparable to the figures in Fig. 1 (Buzeta *et al.* 1974).

The fishing gears, which were used, were of commercial sizes with minor modifications for sampling of 0-group fish. The purse seine was a capelin net 470 meter long and 112 meter deep with a mesh size of 20 mm. In the very end of the bunt a piece of webbing, 28 meter long with mesh size 5 mm, was inserted to prevent the smallest fishes to escape. The pelagic trawl was a capelin trawl, 1000 meshes in circumference with a mesh size of 400 mm, giving an approximate vertical opening of 10—14 meters at 3.5—2.5 knots towing speed. An inner net of mesh size of 12 mm was used in the codend.

The hydrographic stations were worked with Nansen bottles and bathythermograph. Plankton samples were collected with a 180 μ Juday net, hauled vertically from 50 meter to the surface. The light measurements were made at 1 m depth.

RESULTS

HYDROGRAPHY

Fig. 3 shows the drift of the current cross in area 1 and 2. The average velocity of the drogue was 0.1 knot in both areas. In area 3 the displacement of the drogue was less than the error of the positioning.

Fig. 4 shows the vertical temperature distribution in the three areas. In all areas there was a thermocline between 25 and 40 meters, the vertical temperature gradient being more pronounced in area 3 than further west.

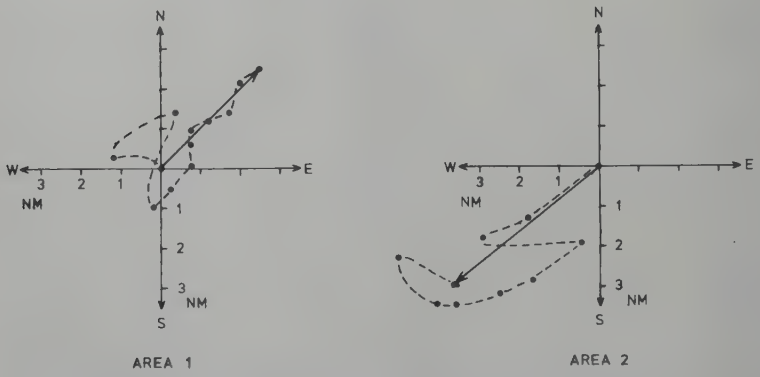

Fig. 3. Drift of drogues during the period of the small scale survey.

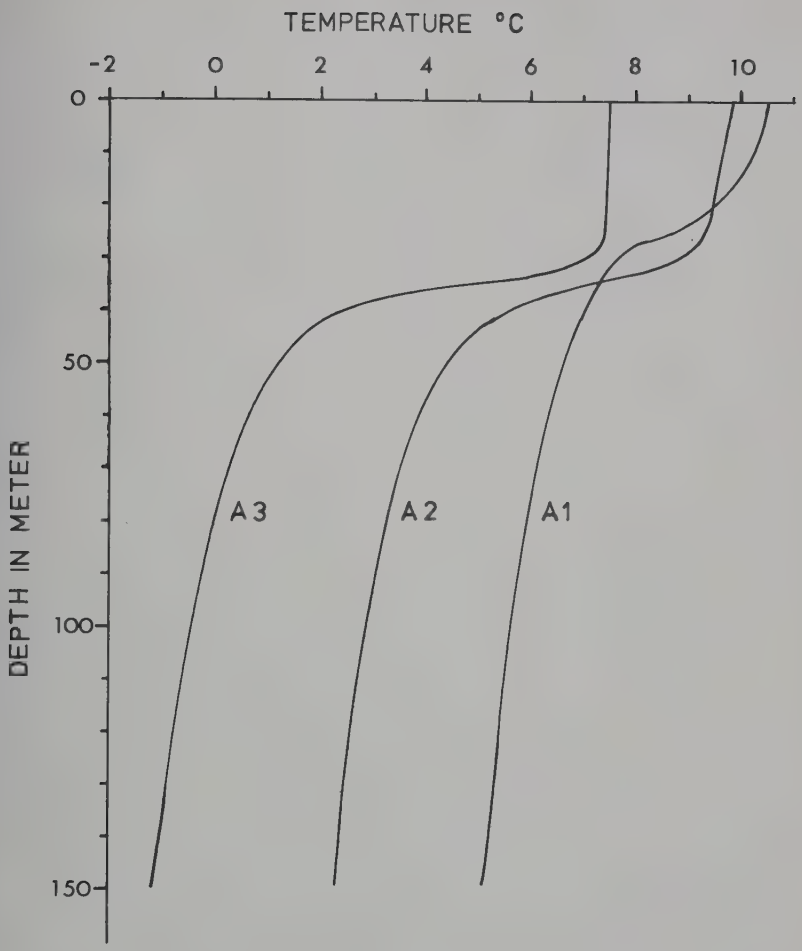

Fig. 4. Vertical distribution of temperature in the three areas.

DISTRIBUTION OF 0—GROUP FISH

The composition of species in the catches are given in Table 1, 2 and 3. According to these tables the distribution of 0-group fish in the three areas can be characterized as follows:

Area 1 was a «pure» redfish area. In area 2 redfish and capelin were mixed while area 3 was a «pure» capelin area. The contribution from other species was quite low compared to the contribution from capelin and redfish.

Table 1. Composition of trawl and purse seine (PS) catches of 0-group fishes in area 1.

St. No.	Date	Hrs. (GMT)	Depth Meters	Redfish		Haddock		Cod		Long Rough Dab		Mackerel	
				No.	%	No.	%	No.	%	No.	%	No.	%
1	27 Aug.	1930	35—48	8 000	100	3	+	2	+	—	—	—	—
2	28 »	0040	25—38	3 000	100	6	+	—	—	—	—	—	—
3	28 »	0547	22—34	1 300	98	9	1	6	+	2	+	14	1
4	28 »	1014	10—22	13 750	100	42	+	5	+	—	—	1	+
5	28 »	1510	25—38	6 000	100	1	+	—	—	—	—	—	—
6	28 »	2108	10—40	1 000	99	8	1	—	—	2	+	—	—
7	29 »	0300	20—40	4 300	100	6	+	—	—	1	+	—	—
8	29 »	0754	10—40	5 600	99	30	1	—	—	—	—	11	+
PS 1	29 »	1814	0—60	25 800	99	181	1	4	+	—	—	—	—
PS 2	29 »	2055	0— 60	52 000	99	460	1	20	+	—	—	—	—

Table 2. Composition of trawl and purse seine (PS) catches of 0-group fishes in area 2.

St. No.	Date	Hrs. (GMT)	Depth Meters	Redfish		Capelin (Unpigmented)		Capelin (Pigmented)		Haddock		Cod		Long Rough Dab	
				No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
11	31 Aug.	2045	25—37	91	+	46 300	99	337	1	6	+	52	+	2	+
12	1 Sep.	0027	22—42	850	3	28 800	97	102	+	5	+	16	+	6	+
13	1 »	0316	15—37	190	95	—	—	—	—	1	+	2	1	6	3
14	1 »	1509	25—42	125	51	110	45	—	—	—	—	1	+	8	3
15	1 »	1919	22—40	135	+	122 400	99	780	1	8	+	24	+	1	+
16	1–2 »	0003	30—42	73	+	71 250	95	3 900	5	2	+	10	+	4	+
17	2 »	0410	10—32	260	22	600	51	271	23	10	1	37	3	1	+
18	2 »	0848	10—25	450	59	—	—	267	35	5	1	35	5	—	—
19	2 »	0957	0—12	—	—	5 000	100	36	+	—	—	1	—	—	—
20	2 »	1544	30—42	7	12	8	14	40	70	1	2	—	—	1	2
21	2 »	2217	10—40	445	+	127 500	99	170	+	3	+	21	+	—	—
22	3 »	0220	30—42	9	45	—	—	—	—	5	25	6	30	—	—
23	3 »	0312	0—12	8 100	45	10 000	56	1	+	4	+	2	+	—	—
PS 3	3 »	1305	0—60	4 200	92	176	4	135	3	34	1	4	+	—	—
PS 4	3 »	1612	0—60	8 700	99	—	—	—	—	41	+	18	+	—	—
PS 5	3 »	2250	0—60	2 700	72	1 000	27	6	+	47	1	17	+	—	—

Table 3. Composition of trawl catches of 0-group fishes in area 3.

St. No.	Date	Hrs. (GMT)	Depth	Capelin (Unpigmented)		Capelin (Pigmented)		Cod		Long Rough Dab	
				No.	%	No.	%	No.	%	No.	%
24	5 Sept.	1526	0—12	49 000	100	151	+	—	—	—	—
25	5 Sept.	1919	0—12	10 000	100	33	+	—	—	—	—
26	5 Sept.	2255	20—35	13 800	86	2 120	13	100	1	2	+

Fig. 5 shows selected typical echograms from the areas. It appears from the paper record that the redfish in area 1 had a rather wide spread vertical distribution in daylight, but concentrated in the upper layer at dark. This is also clearly demonstrated in Fig. 6 where the contributions from the different echo integrator channels are presented as a function of time. During the dark 80—100% of the reflecting scatterers were observed in the upper channel, 6—15 m. The total echo abundance showed no significant diel variation.

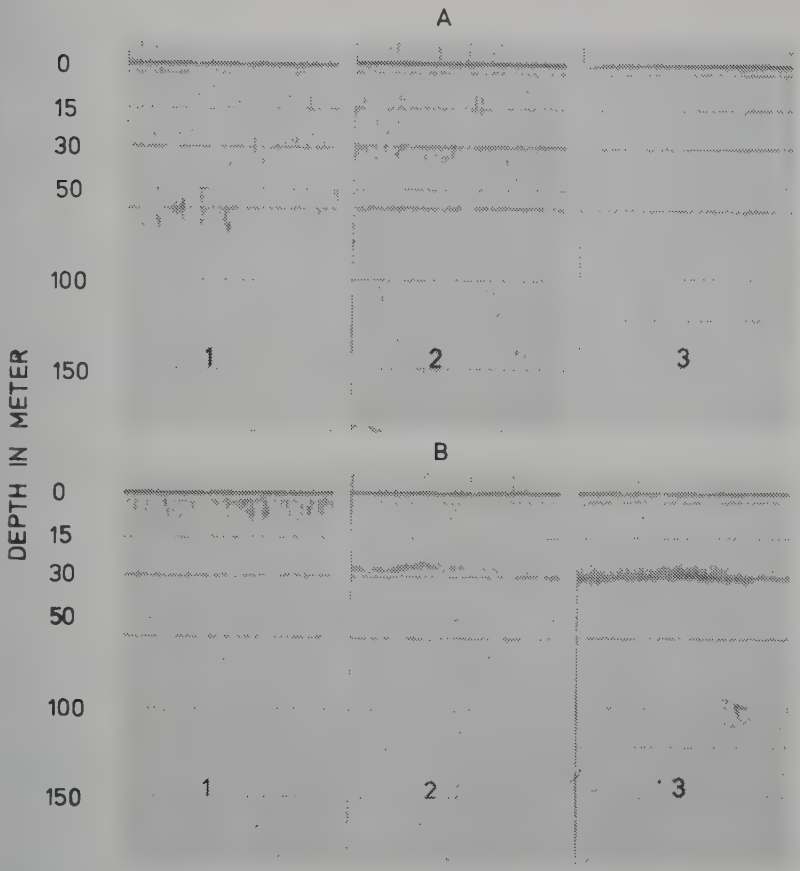

Fig. 5. Typical echo recordings from the three areas. A) Daylight, B) at dark. 1) Area 1, 2) area 2, 3) area 3.

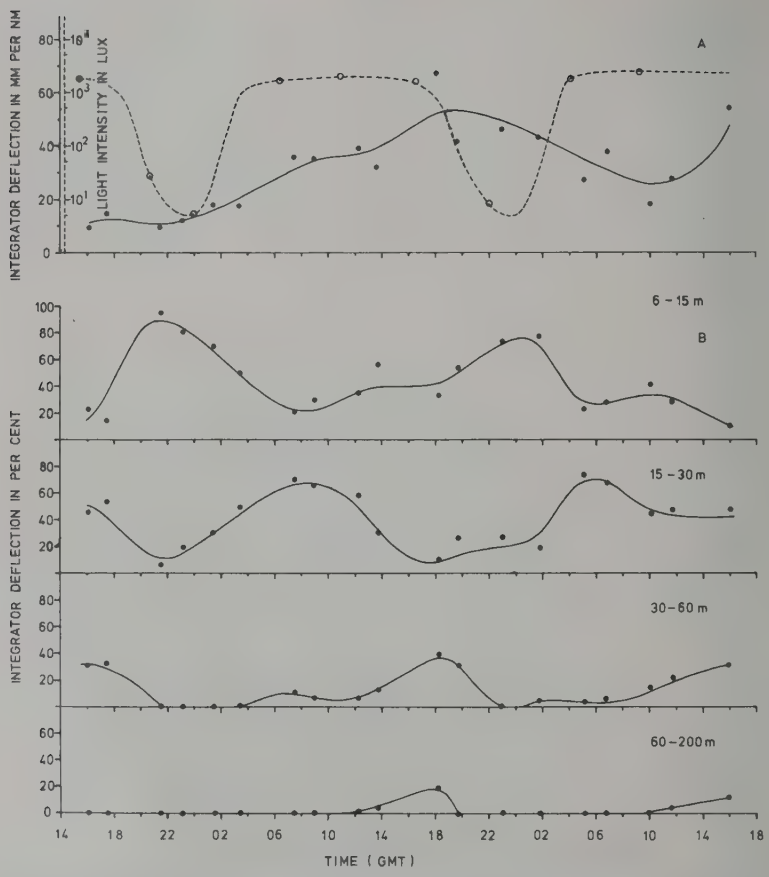

Fig. 6. A) Total echo abundance and light intensity according to time in area 1. B) The contribution to the total echo abundance from various depths according to time.

In area 2 a significant diel variation in echo abundance was observed (Fig. 7). The integrator deflection was significantly higher at dark than in daylight. There was also a periodic variation in species composition in the catches from the 10—30 m depth layer (Table 2, Fig. 8). In this layer the redfish were caught in daylight while at dark the catches consisted of capelin and krill. Capelin were also caught at the very surface (0 –12 m) in daylight. The observations made by the scuba divers verified these observations. At dark they found a scattering layer of krill and capelin in 20 –30 m while the redfish were observed very close to the surface, 0 –2 m. In daylight they saw no 0-group fish at all.

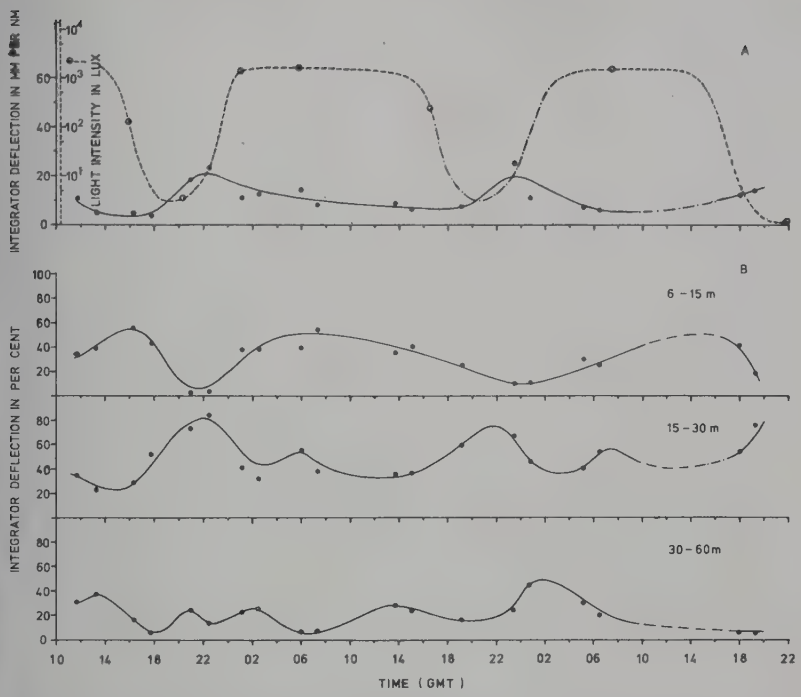

Fig. 7. A) Total echo abundance and light intensity according to time in area 2. B) The contribution to the total echo abundance from various depths according to time.

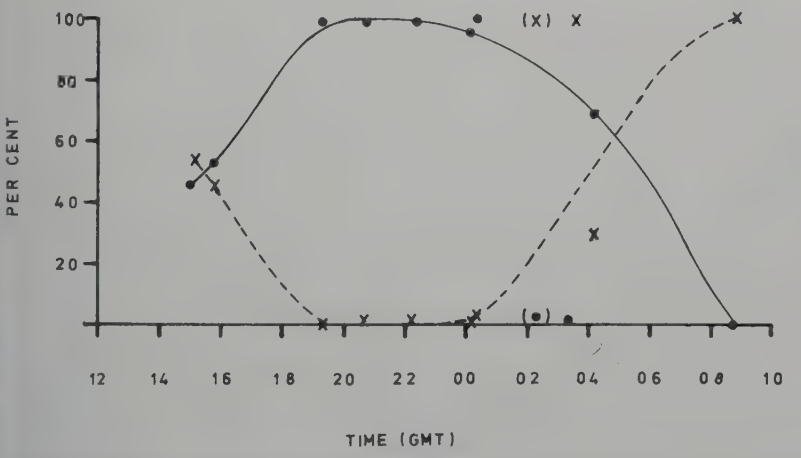

Fig. 8. The fish composition of trawl catches from 10 to 30 m depth in area 2. Solid line) capelin, broken line) redfish.

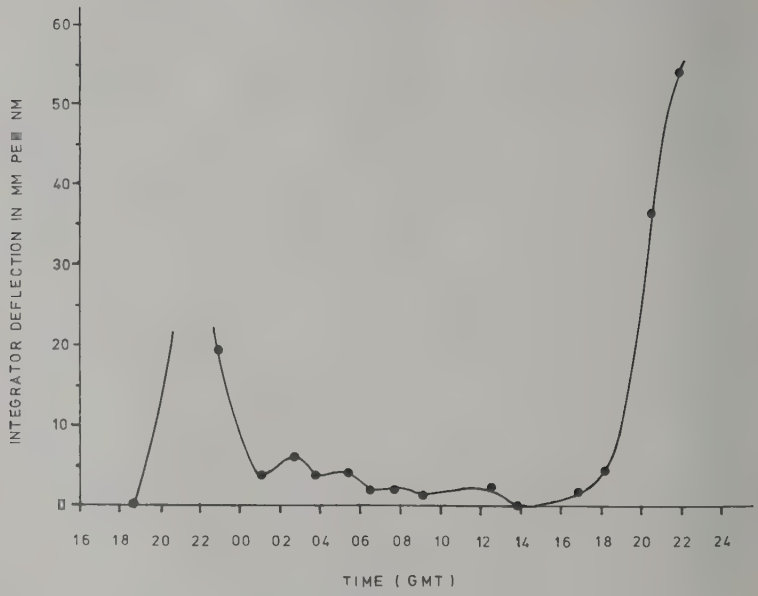

Fig. 9. Total echo abundance according to time in area 3.

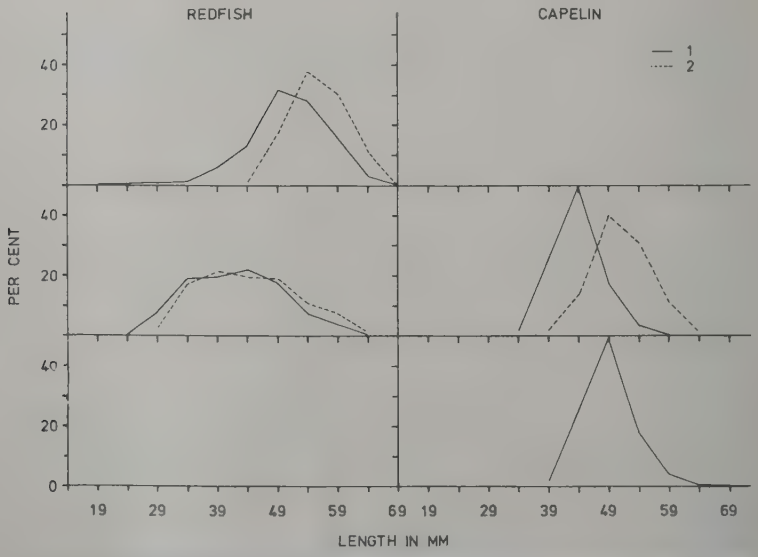

Fig. 10. Length distributions of 0-group redfish and capelin in the different areas. 1) Pelagic trawl, 2) purse seine.

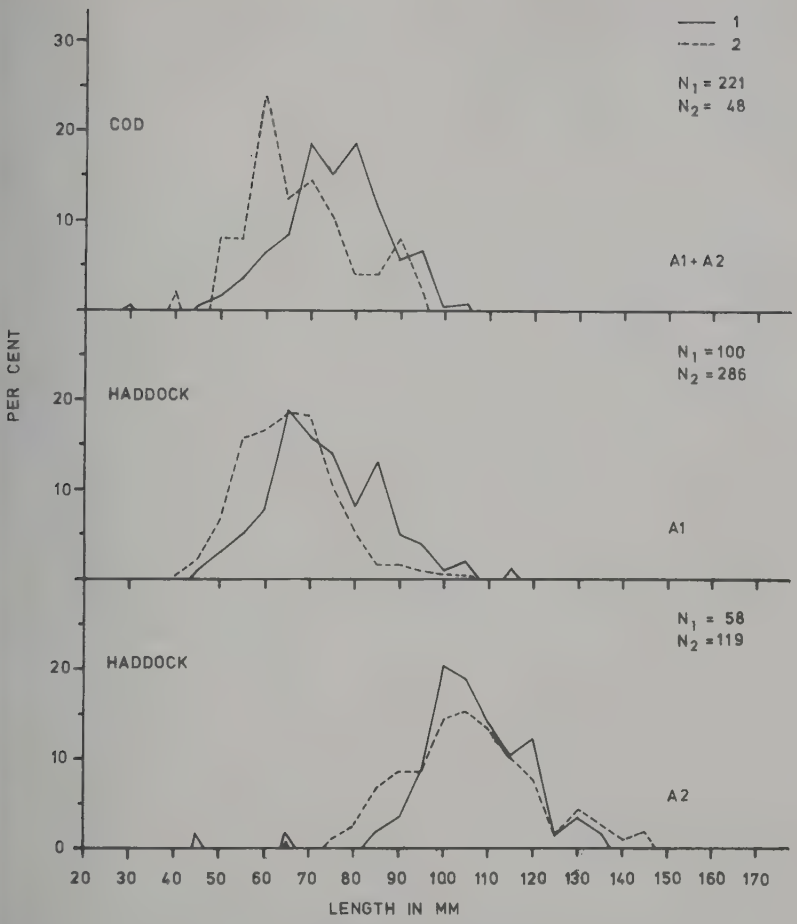

Fig. 11. Length distributions of 0-group cod and haddock in the different areas. 1) Pelagic trawl, 2) purse seine.

In area 3 there was practically no contribution to the echo abundance in daylight (Fig. 9), but great numbers of 0-group capelin were caught in surface hauls (Table 3). At dark the scattering layer in 20—30 m depth consisted of capelin and krill (Fig. 5.3 and Fig. 9) which was sampled with pelagic trawl and observed by scuba divers.

Nearly all the observed 0-group capelin were unpigmented while the 0-group redfish, cod and haddock were pigmented. Fig. 10 and 11 show the length distributions of these four species according to area and gear.

The krill, mainly *Thysanoessa sp.*, were only caught at dark in the pelagic trawl, sometimes in quantities up to 80 kg per haul in area 2. It had an average length of about 2 cm.

DISCUSSION

Table 1, 2 and 3 show that 0-group redfish and capelin dominated the catches completely. Fig. 5, 7 and 8 show that 0-group redfish and unpigmented 0-group capelin had a different vertical migration pattern. The redfish showed a normal diel vertical migration and were found in the surface layer at dark while the capelin stayed in the surface layer during the daylight period and descended to deeper water at dark. According to BREDER (1962) the light radiation in the upper water layers may have deleterious effects on pigmented organisms while unpigmented organisms to some extent are protected against the light radiation. This may explain why capelin was found at the very surface in broad daylight. By staying in the uppermost water layer the unpigmented larvae can feed almost undisturbed by fish predators during most of the daylight period. However, the radiation theory cannot explain why the capelin descended and consentrated at the thermocline at dark (Figs. 4 and 8). A possible explanation may be that in the dark period, when feeding is difficult, the larvae save energy by staying in layers of higher water density. This behaviour will also be of advantage if the predators migrate to the surface layer at dark. It is known that 0-group cod feed on capelin larvae, and it is also likely that 0-group haddock do so, but the data at hand on the diel vertical migration of the two latter species are insufficient.

The observations of krill indicated that it stayed in depths below 40 m in daylight while it mixed with the 0-group capelin in the thermocline at dark (Fig. 5.3). The higher integrator deflection at dark in area 2 and 3 (Figs. 7 and 9) are thus caused by this mixture.

Although the observations on the horizontal distribution pattern (patchiness) of 0-group redfish and capelin are limited, some main features were found. Fig. 5 shows that 0-group redfish gathered in small groups during the daylight period. Some observations indicated a similar grouping of 0-group capelin. A lot of small sonar echoes in the uppermost water layer in daylight and the fact that the scuba divers did not observe 0-group capelin, in daylight supports this view. When the fishes form schools, the propability of detecting them with echo sounders is less than when they are evenly distributed, and dispersed distributions at dark are therefore easier to detect than dense schools in daylight. At dark the capelin dispersed in 20—30 m depth. The redfish, which at dark were observed by eye in the surface layer, appeared also to be dispersed although

Fig. 5.1 indicates that a certain grouping was maintained even in the most dark period. The differences in fish length between purse seine and trawl catches, which occur in Fig. 10 and Fig. 11, are not significant. From the present investigation we must thus conclude that the trawl catches were representative samples of the length distributions of 0-group fish.

The 0-group capelin, which in broad daylight is found above the depth of the hull mounted transducers, will not be recorded by the echo sounder (Fig. 5.3). Neither will it be representatively fished by a pelagic trawl unless special care is taken to haul the trawl at the very surface. Therefore errors of unknown magnitude might be introduced to the indices of abundance for 0-group capelin.

The redfish, which is spread in the water column during the daylight period, will be detected by echo sounders most of the time (Fig. 5.1). Although there might be areas where this species is not seen by echo sounders during a small part of the dark period, like area 2, it is felt that the error introduced to the abundance indices are negligible in comparison with the 0-group capelin.

To get a better understanding of the observed vertical diel migration pattern of 0-group capelin more detailed information is needed both on the distribution of plankton and the distribution and stomach contents of fishes in the upper 50 m depth layer in the Barents Sea.

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ABUNDANCE ESTIMATES OF THE SPAWNING STOCK OF BLUE WHITING *(MICROMESISTIUS POUTASSOU* (RISSO, 1810)) IN THE AREA WEST OF THE BRITISH ISLES IN 1972—1974

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ABSTRACT

Buzeta, R. and Nakken, O. 1975. Abundance estimates of the spawning stock of blue whiting (*Micromesistius poutassou* (Risso, 1810)) in the area west of the British Isles in 1972—1974. *FiskDir.Skr.Ser.HavUnders.*, *16* : 000—000.

An analysis is made on the blue whiting data from the echo surveys conducted during 1972—1974 for assessment of the spawning stock west of the British Isles.

Acoustic data are evaluated using a length dependent density coefficient.

Area and time coverage are discussed for each survey. Mean density and total abundance are calculated for the three years in the investigated area, and a stock size of approximately 6 million tons is suggested for the spawning stock.

INTRODUCTION

The stock of blue whiting has been surveyed for the last three years during the spawning period using the research vessel «G. O. Sars» (Jakupsstovu og Midttun 1972, Midttun and Nakken 1973, Buzeta *et al.* 1974). The survey grid, trawl stations and fish distribution are shown in Fig. 1—3. The technique applied is described by Forbes and Nakken (1972), Midttun and Nakken (1973) and Dommasnes and Nakken (1975). The concentrations of spawning blue whiting have been surveyed twice each year — from the Shetland area and southward to 52° N and then northward again. Abundance estimates based on echo integrator data have been worked out for each survey (Midttun and Nakken 1973, Buzeta *et al.* 1974). These estimates are listed in Table 1. The figures show large variation, both within and between years. They are, however, based on the assumption that the scattering cross section of blue whiting is proportional to its weight, a rather rough approximation. Both the area and time coverage of the survey have varied from year to year. The time of maturing and accordingly the amount of fish on the spawning grounds may have varied from survey to survey, and the estimates should therefore be considered as fractions of the total spawning stock. In the present paper the acoustic and biological material from the cruises are analyzed in more detail, and some of the factors affecting the fluctuation of the abundance estimates are discussed.

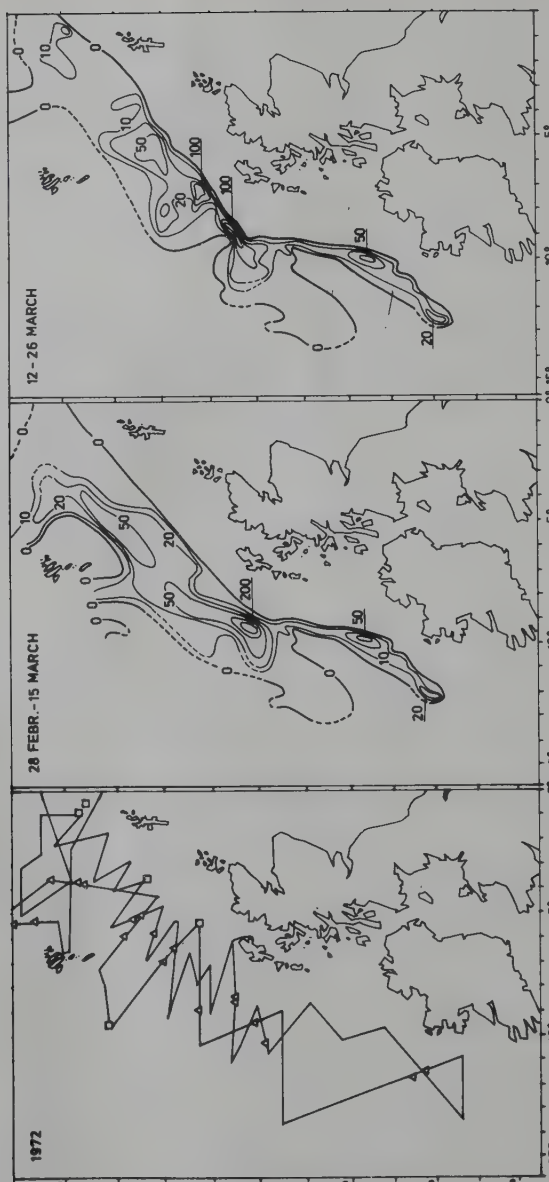

Fig. 1. Survey grid, trawl stations and distribution of integrated echo intensity (mm deflection) in 1972.

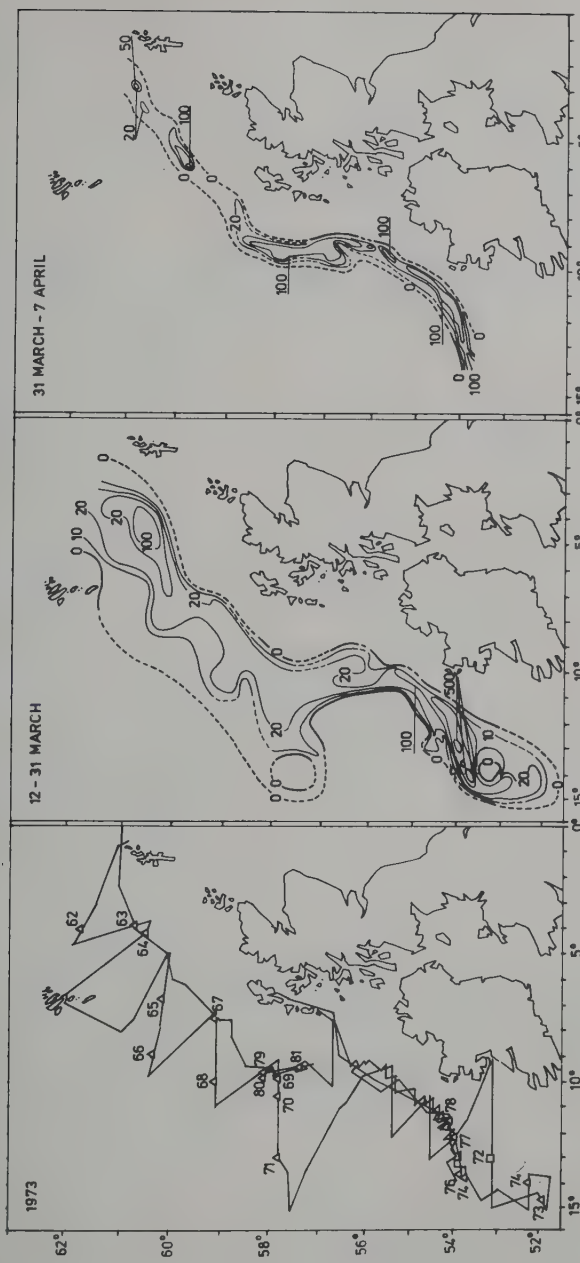

Fig. 2. Survey grid, trawl stations (numbered) and distribution of integrated echo intensity in 1973.

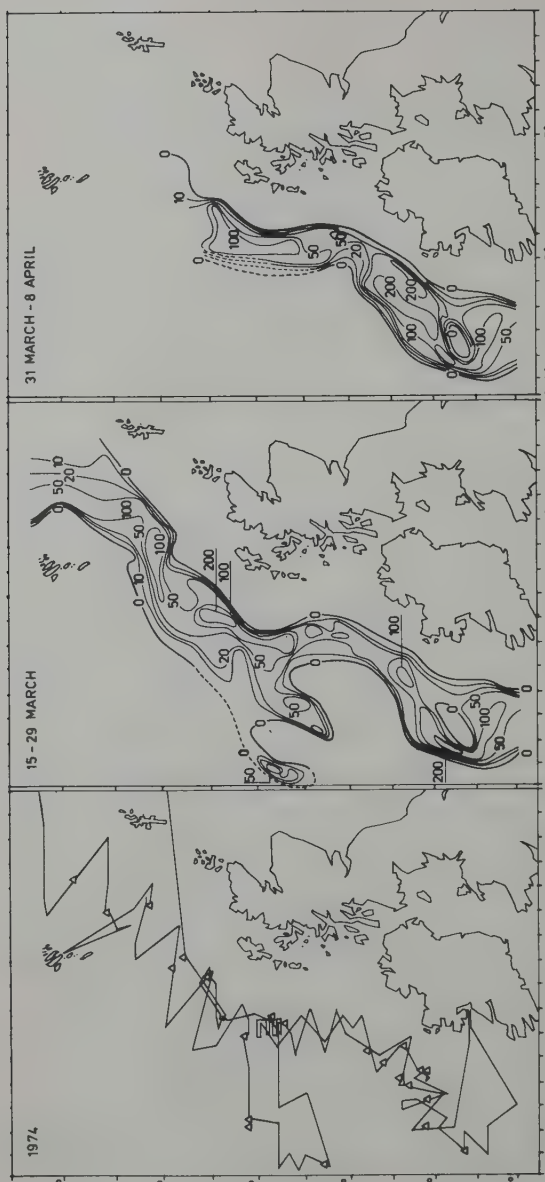

Fig. 3. Survey grid, trawl stations and distribution of integrated echo intensity in 1974.

MATERIAL AND METHOD

The method applied during the acoustic surveys is described by Forbes and Nakken (1972) and Midttun and Nakken (1973). More details are given by Craig (1973) and Dommasnes and Nakken (1975). The relation between fish density, ϱ_A, and integrated echo intensity, M, is:

$$\varrho_A = C \cdot M + b \qquad \text{(I)}$$

where ϱ_A is the number of fish per unit area and M is the integrated echo intensity. The density coefficient C represents the density of fish causing 1 mm deflection on the echo integrator, and it is a constant as long as fish specie and size remains constant. The constant b is a treshold density. Below this there is no contribution to the integrated echo intensity.

When three size groups of fish contribute to M, the following expressions for the density of fish within each size group are valid (Dommasnes and Nakken 1975):

$$\begin{aligned} \varrho_{A1} &= k_1 \cdot K \cdot M \\ \varrho_{A2} &= k_2 \cdot K \cdot M \\ \varrho_{A2} &= k_3 \cdot K \cdot M \end{aligned} \qquad \text{(II)}$$

and

$$K = \frac{C_1 \cdot C_2 \cdot C_3}{k_1 \cdot C_2 \cdot C_3 + k_2 \cdot C_1 \cdot C_3 + k_3 \cdot C_1 \cdot C_2}$$

where k_i is the percentage of the i-th sizegroup in the catches, and C_i is the value of C for the length L_i. The numerical values of the density coefficient, C_i, are found from a L—C cruve (Fig. 4).

The total number of fish in the i-th sizegroup within an area A is given by

$$N_i = \int_A \varrho_A da = \overline{k_i \cdot K} \int_A M \cdot dA \qquad \text{(III)}$$

where the bar denotes the average over the area A. Finally, the total weight of each sizegroup is found by applying a weight—length relationship. Due to the relative low number of trawl stations, length data from the whole area were pooled each year, and consequently k_i and C_i were averaged over the whole investigated area.

RESULTS

The abundance estimates, which are given in Table 1, were recalculated according to the procedure outlined above. The relation between the density coefficient and the length of blue whiting is shown in Fig. 4.

Table 1. Estimates of abundance and mean density from the different surveys (Midttun and Nakken 1973, Buzeta *et al.* 1974).

Year	Survey	Period	Trawl station	Area (NM^2)	Abundance (Ton)	Density (Ton/NM^2)
1972.....	1 (S)	28.2—15.3	20	41 940	4.4×10^6	104.9
	2 (N)	12.3—26.3	11	33 090	2.7×10^6	81.6
1973.....	3 (S)	12.3—30.3	17	94 500	10.7×10^6	113.2
	4 (N)	31.3— 7.4	3	12 960	4.0×10^6	208.6
1974.....	5 (S)	15.3—29.3	16	67 500	1.8×10^6	36.6
	6 (N)	31.3— 8.4	8	34 950	1.8×10^6	51.5

(S) Southward crossing.
(N) Northward crossing.
NM Nautical mile.

The curve is based on the target strength—length relationship reported by Nakken and Olsen (1973) and on the values of the density coefficient arrived at by Midttun and Nakken (1973) and Buzeta *et al.* (1974). The change in the ordinate scale from 1973 to 1974 is caused by a change in the settings of the echo sounder onboard the «G. O. Sars».

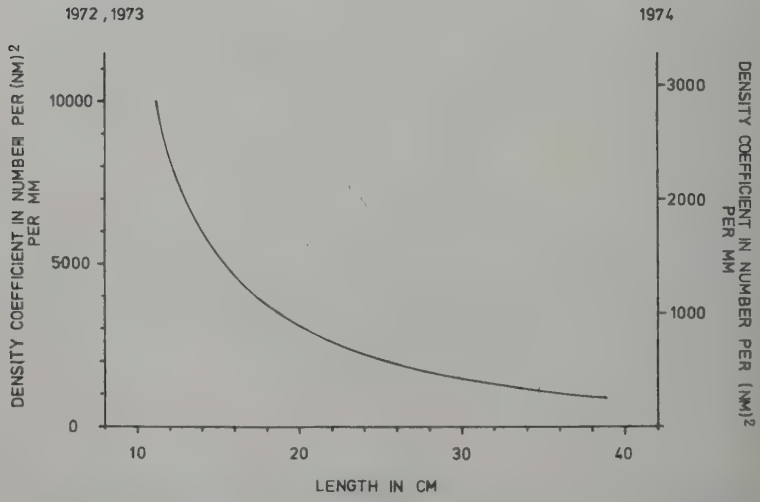

Fig. 4. The density coefficient C as a function of length for blue whiting the different years.

The length distributions of the blue whiting are given in Fig. 5. In these distributions the three modal groups were selected as size-groups, and *C*-values corresponding to the modal lengths were found in Fig. 4. The values of *k* were also found from the length distributions in Fig. 5 by accumulation of the percentages within each modal group. The age of the fish within each of the three modal length groups was found from Fig. 6. This figure shows the age—length relationship for blue whiting as per available literature.

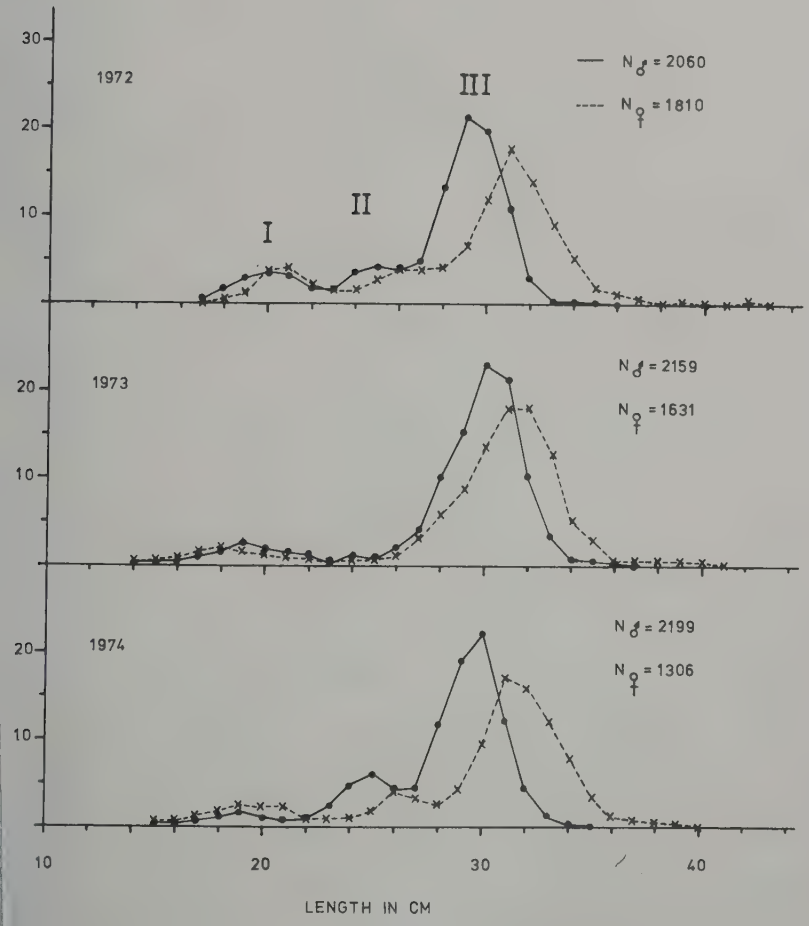

Fig. 5. Length distribution of blue whiting in the samples. (I, II and III are modal lengths).

Table 2. Estimated weights (gr) of blue whiting according to length the different years.

Year	Length (cm)													Weight-length relationship and correlation coefficient
	14	16	18	20	22	24	26	28	30	32	34	36	38	
1972			33	46	63	82	106	134	166	203	246	295	349	$W = 0.0037\ L^{3.15}\ r = 0.99$
1973	14	22	32	45	61	81	105	134	167	206	250	301	359	$W = 0.0028\ L^{3.24}\ r = 0.99$
1974		23	33	46	61	80	102	128	159	194	233	278	329	$W = 0.0045\ L^{3.08}\ r = 0.99$

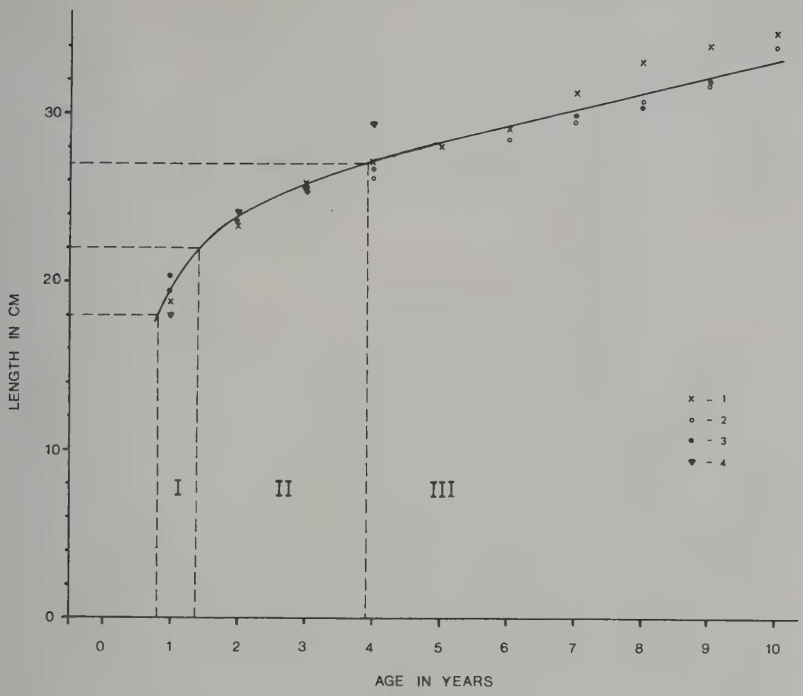

Fig. 6. Blue whiting growth curve (Data in RAITT 1968).
1) The western coast of Scotland (RAITT 1966),
2) the Færoes (RAITT 1966),
3) Iceland (RAITT 1966),
4) Iceland (SÆMUNDSSON 1929).
I, II and III are modal lengths according to length distribution in the samples.

The weight—length relationship of blue whiting for the three years are shown in Table 2. The figures in the table are estimated weights using the length-weight equation.

In Table 3 are listed the observed values of the different parameters used in the calculations and the estimates of abundance for each size-group and year.

Table 4 gives the total abundance in number and tons, the sampled area and the average density in tons per unit area for the three years. The percentages of fish in the different maturity stages are also shown in Table 4. From the correlative changes in percentage from mature to spent fish between the first and the second part of the cruise the top of the spawning season is indicated.

Table 3. Corresponding values of modal length (L), density coefficient (C), calculated weight (W), length frequency (k) and relative and absolute abundance in each modal length group the different years.

Year	L (cm)	C (n/mm/(nm)²)	W (gr)	k %	Relative abundance (mm.(nm)²)	Absolute abundance (number)	Absolute abundance (tons)
1972...	20	3 200	46	13	$11 . 10^6$	$2.2 . 10^9$	$0.10 . 10^6$
	25	2 100	93	9		$1.7 . 10^9$	$0.16 . 10^6$
	30	1 500	166	78		$14.3 . 10^9$	$2.37 . 10^6$
1973...	18	3 700	32	10	$26 . 10^6$	$4.1 . 10^9$	$0.13 . 10^6$
	30	1 570	167	90		$38.9 . 10^9$	$6.49 . 10^6$
1974...	19	1 133	39	9	$31 . 10^6$	$1.5 . 10^9$	$0.06 . 10^6$
	25	700	91	18		$3.1 . 10^9$	$0.28 . 10^6$
	30	500	159	73		$12.4 . 10^9$	$1.97 . 10^6$

Table 4. Calculated abundance, density and observed maturity of sampled fish in per cent on the different cruises.

Year	Survey	Sampled area (nm²)	Abundance (Tons)	Density (Ton/nm²)	Maturity I	Maturity M	Maturity S
1972.....	1 (S)	41 940	2.6×10^6	62.6	19	75	6
	2 (N)	33 090	1.6×10^6	49.1	36	46	18
1973.....	3 (S)	94 500	6.6×10^6	70.1	75	22	3
	4 (N)	12 960	2.4×10^6	190.4	1	77	22
1974.....	5 (S)	67 500	2.3×10^6	34.4	67	29	4
	6 (N)	34 950	2.3×10^6	66.0	8	64	28

(S) Southward crossing, (N) Northward crossing, I = Immature, M = Mature, S = Spent.

Table 5. Maturity distribution (%) and mean length (cm) in the samples from cruise 3 and 4 (1973). Area south of 59 °N.

Maturity	Cruise 3 Trawl Station 69—71 %	Cruise 3 Trawl Station 69—71 cm	Cruise 4 Trawl Station 72—80 %	Cruise 4 Trawl Station 72—80 cm
Immature*	43.3	31	0.8	30
Matur	56.7	30	76.6	29
Spent			22.2	30

* Juveniles (<22 cm) disregarded.

In 1973 the maturing process was investigated in details. Table 5 shows the percentages and mean lengths of fish at each maturity stage in different periods of time. It appears that the fish changes from the prespawning stage into the stages spawning and spent within a very short period (time difference between St. 71 and 72 is one week). There were no significant differences in mean lengths between prespawning, spawning and spent fish.

DISCUSSION

The estimates of abundance, calculated here, tend to be lower than the previous. The main reason for this is that the previous estimates were obtained under the assumption that all fishes were reflecting as if they were 30 cm in length. As the smaller fish will contribute more per unit weight to the echo integrator output than the larger one, the estimates will be reduced when a length dependent density coefficient is used. The variation from survey to survey is still present to a considerable extent, and in the following some possible reasons for this variation are discussed.

In the introduction the grid coverage is mentioned as a possible source to large variances. To assess the blue whiting spawning stock abundance, the best procedure will be to cover most of the spawning grounds during the period when most of the spawning stock is present on these grounds.

There is no doubt that the cruises satisfactory cover large parts of the spawning area at least for some of the surveys. This is evident from maps of larvae distribution (Bainbridge and Cooper 1973) which show that Rockall and Porcupine banks and the continental margin of the south-western Celtic Sea are the main spawning grounds for blue whiting. It can, however, be questioned whether both the area and time coverage are sufficient for any of the surveys.

Table 1 shows the sampled areas on each cruise. According to this table the widest coverage were made during cruise number 3 (1973) and cruise number 5 (1974). Although the main spawning areas were covered in 1972, the coverage of the Rockall and Porcupine banks was very poor that year.

To find which survey has the best time coverage, it is necessary to analyse the maturity distribution in the samples. The highest percentage of mature fish will be an indication of the peak of the spawning, and table 4 shows that the higher percentage of mature fish coincide with the higher density values.

It is difficult to say whether the spawning takes place massively or by consecutive groups of spawners entering the spawning ground. A short

duration of the spawning period is suggested as some of the cruises have missed by days the peak of the spawning season (Buzeta *et al.* 1974) and also because of the quick maturing process during cruise 3 and 4 (1973). This indicates a massive spawning.

Cruises 1, 4 and 6 seem to have the best time coverage as most of the fish were in a spawning stage, which would mean that most of the spawning stock was present at the time of the investigation. With the exception of cruirse number 4 the mean densities are also similar. Cruise 4 (1973) has a much higher density owing to a selection of course lines through the most dense concentrations. A high percentage of immature fish is present in the samples on cruise 3 (Table 4). The size distribution of these fish was investigated to see if the mature fish in the 2nd part was different from these immature fish. Table 5 shows that it is the same group of fishes. Cruise 3 (1973) is therefore chosen as the best abundance estimate assuming that during this survey, when most of the spawning ground was covered, the major part of the spawning stock was already present.

Although there is a small amount of juvenile fishes in the samples, most of the fish entering the area are spawners. When the size distribution of the fish (Fig. 5) is compared with the age-length curve in Fig. 6, mode I represents fishes of 1 year which are not spawning and thus are not quantitatively well represented in the samples. Modal size II representing fish of 2—3 years, which is the approximate age of first maturity (Raitt 1968), is also poorly represented in the spawning area. (Fig. 5). Thus the bulk of the spawning stock is represented by fish of ≥ 4 years (mode III). This fish spawn on the continental slope west of the British Isles and on the Porcupine, Rockall and Rose Mary banks, an area representing roughly 90.000 square nautical miles. The mean density, attained by the fish on the peak of the spawning season, is around 70 ton per square nautical miles which means that the size of the spawning stock is of the order of 6 million tons.

The fluctuation of the total spawning stock abundance between years should be studied in the light of the strength of the age groups of spawners since the age composition of the spawning stock may vary between years, i.e. scarce amount of 2—3 years spawners in 1973 (Fig. 5).

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QUANTITATIVE DISTRIBUTION OF ZOOPLANKTON IN THE COAST AND BANK AREAS OF WESTERN AND NORTHWESTERN NORWAY DURING MARCH—JUNE 1959—1966

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ABSTRACT

WIBORG, K. F. 1976. Quantitative distribution of zooplankton in the coast and bank areas of western and northwestern Norway during March—June 1959—1966. *FiskDir. Skr. Ser. HavUnders.*, *16*: 259—277.

During March—June 1959—1966 the coastal banks off western and northwestern Norway were surveyed for fish eggs and larvae. Zooplankton was sampled with Juday nets, Nansen nets and Clarke-Bumpus plankton samplers. The sample volumes were measured by displacement. From the end of March to the middle of April volumes were below 10 ml/m^2 of sea surface except for local patches of prespawning *Calanus finmarchicus* where there were up to 90—110 ml/m^2 with maximum concentrations of 3 ml/m^3. After the middle of April volumes increased to average 25—50 ml/m^2 with maxima of 100—200 ml/m^2 and concentrations of up to 4—7 ml/m^3.

Similar conditions persisted throughout May. On the northern banks the increase in sample volumes was most marked in June. *C.finmarchicus* was generally the dominant species. On the southern banks stage V copepodites and females of the wintering generation were in majority at the end of March — beginning of April, while stages III—IV of the spring generation were predominant in the middle of April, progressing to stages IV—V at the end of the month. On the northern banks the development was slower, stages II—III still dominating at the end of April. The total standing stock of zooplankton in the coast and bank areas between Stad and Andenes in April—June is estimated to be of a size order of 7×10^6 t weight and for the entire coastal area of Norway 13×10^6 t. The total annual production of zooplankton along the coast of Norway based on the figures of TIMOKHINA (1964) is estimated to be 26×10^6 t and when based on a primary production estimate of 100 g C/m^2/year (RYTHER 1969), 25—50 $\times 10^6$ t.

INTRODUCTION

During the years 1959—1966 the coast and bank areas of western and northwestern Norway were surveyed during the spring months for fish eggs and larvae. Reports have been published (DRAGESUND 1965, DRAGESUND and HOGNESTAD 1966 and 1967, DRAGESUND and WIBORG

1963, WIBORG 1960 b, 1961, 1962 a). In addition to the eggs and larvae of fish, zooplankton samples were also analyzed, and these results are presented in this paper.

MATERIAL AND METHODS

Samples were taken in oblique hauls with a Clarke-Bumpus plankton sampler (CB) in the upper 50 m and in vertical hauls from bottom to surface or 200 (100)—0 m with various nets, Nansen 70 cm (N 70), Juday 80 cm (J 80), Juday 36 cm (J 36) and a one meter egg net (0/100). The mesh sizes used were: in J 36 — 180 µ, N 70 — 180 µ and 500 µ J 80, 0/100 and CB — all 500 µ.

The samples were preserved in 4% formaldehyde. After removal of fish eggs and larvae the zooplankton volumes were measured by displacement (ROBERTSON 1970) and volumes calculated per m^2 of sea surface of per m^3 of sea water.

Biomass determination by volume incorporates measurements of the highly variable water and ash contents of the plankton organisms and therefore does not give an accurate picture of their nutritional state or potential values as food (STEEDMAN 1974). The plankton samples were also taken with different types of gear and in various kinds of hauls and therefore are not strictly comparable. However, as the zooplankton was fairly uniform, being mainly composed of copepods and other crustaceans, the figures will indicate the relative biomass of plankton on the Norwegian coastal banks during the spring and early summer.

The main data are presented in Fig. 1—7 and Table I.

RESULTS

1959

(0/100, 100—0 m. Fig. 1 A.)

During the first half of April the plankton was generally scarce, less than 20 ml/m^2, except near the slope off Røst—Vesterålen with figures of about 50 ml/m^2. Further south, at Stad—Ona, volumes exceeded 20 ml/m^2 at a few stations, and *Calanus finmarchicus* adults and stage V copepodites predominated.

During the second half of April volumes increased to 40—45 ml/m^2 of Stad and Ona and near the slope farther north up to 60 ml/m^2, but were much lower elsewhere.

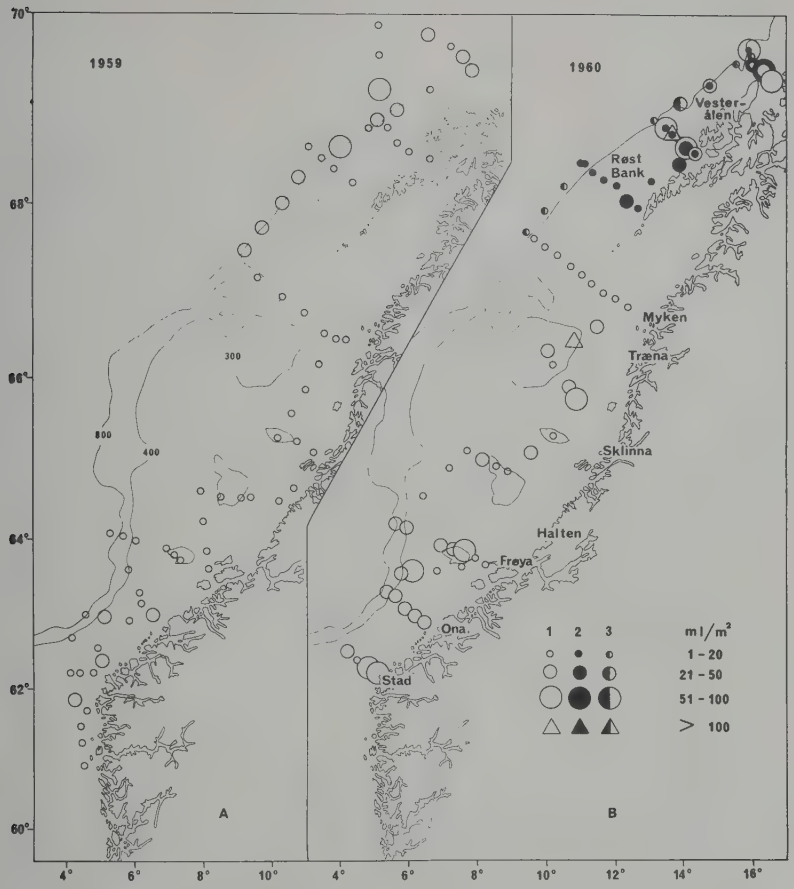

Fig 1. Zooplankton volumes, ml/m² of sea surface.
A) 1959, 0/100, 100—0 m. 18—29 April. B) 1960, CB, 50—0 m. 1) 25 May—2 June. 2) 7—10 June. 3) Equal volumes in both periods.

1960

(CB upper 50 m. Fig. 1 B.)

At the end of March less than 10 ml/m² were taken in the upper 50 m. At the end of May — beginning of June maxima of 180 and 120 ml/m² were recorded at Stad—Ona and Vesterålen banks respectively. Maximum concentrations in the upper 25 m were 5 ml/m³ off Vesterålen, 6.6 ml/m³ off Træna and 2.9 ml/m³ off Ona.

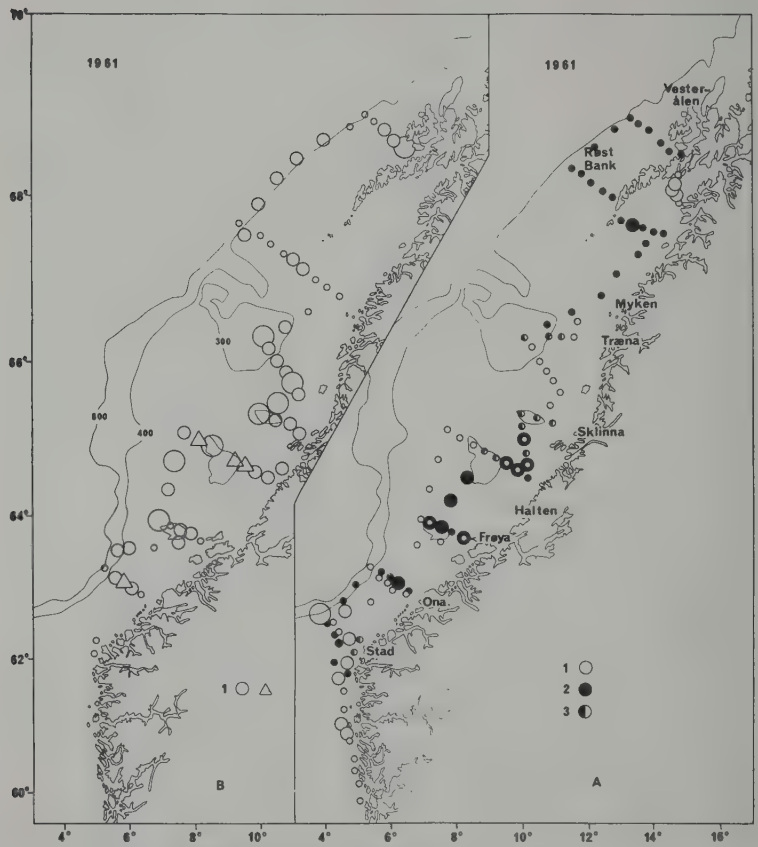

Fig. 2. Zooplankton volumes, ml/m² of sea surface.
A) 1961, J 36, bottom to 0 m. 1) 6—19 April. 2) 20—29 April. 3) Equal volumes in both periods. B) 1961, CB, 50—0m, 25 May—3 June. Symbol size as in Fig. 1.

1961

(J 36 and N 70, bottom to 0 m, and CB in the upper 50 m. Fig. 2.)

During April, plankton was generally scarce. At the end of May-beginning of June *C.finmarchicus* predominated, with maxima of 100—150 ml/m² between Stad and Halten. Farther north, figures were mostly below 50 ml/m² with the exception of a few rich hauls with 60—100 ml/m² off Sklinna and Træna. Maximum concentrations were 3.7 ml/m³ in the Ona—Frøya area, 5.2 ml/m³ on the Sklinna and Halten banks and 2.0 ml/m³ on the Røst bank.

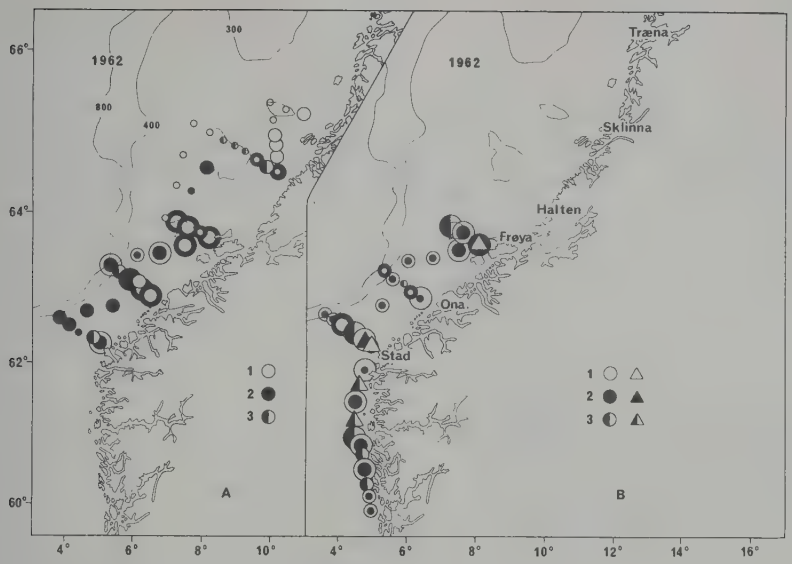

Fig. 3. Zooplankton volumes, ml/m² of sea surface.
A) 1962, J 36, bottom to 0 m. 1) 2—7 April. 2) 9—12 April. 3) Equal volumes in both periods. B) 1962, 24—27 April. 1) CB, 50—0 m. 2) J 36, bottom to 0 m. 3) Equal volumes in both gears. Symbol size as in Fig. 1.

1962

(J 36, bottom to 0 m, and CB in the upper 50 m. Fig. 3.)

At the beginning of April evidently most of the plankton was concentrated below 50 m as the J 36 nets yieled up to 60—90 ml/m², CB hauls less than 20 ml/m², but the J 36 net may also have caught more plankton because of the smaller mesh. At the end of April both types of gear caught approximately equal volumes/m² sea surface, and the plankton was also more abundant; 50—160 ml/m² between the Sognefjord and Stad, 60—120 ml/m²off Frøya. Maximum concentrations in two areas were 7.0 and 4.0 ml/m³ respectively.

1963

(N 70, J 80 and J 36, 100—0 m, CB in the upper 50 m. Fig. 4 A.)

At the beginning of April a patch of prespawning *C. finmarchicus* off Stad yielded 109 ml/m² and 3.4. ml/m³. In other areas the plankton was scarce, with maxima of 20—25 ml/m². During the second half of April plankton was scarce except off Frøya where 50— 80ml/m² and 2.5 ml/m³ were recorded in the upper 25 m.

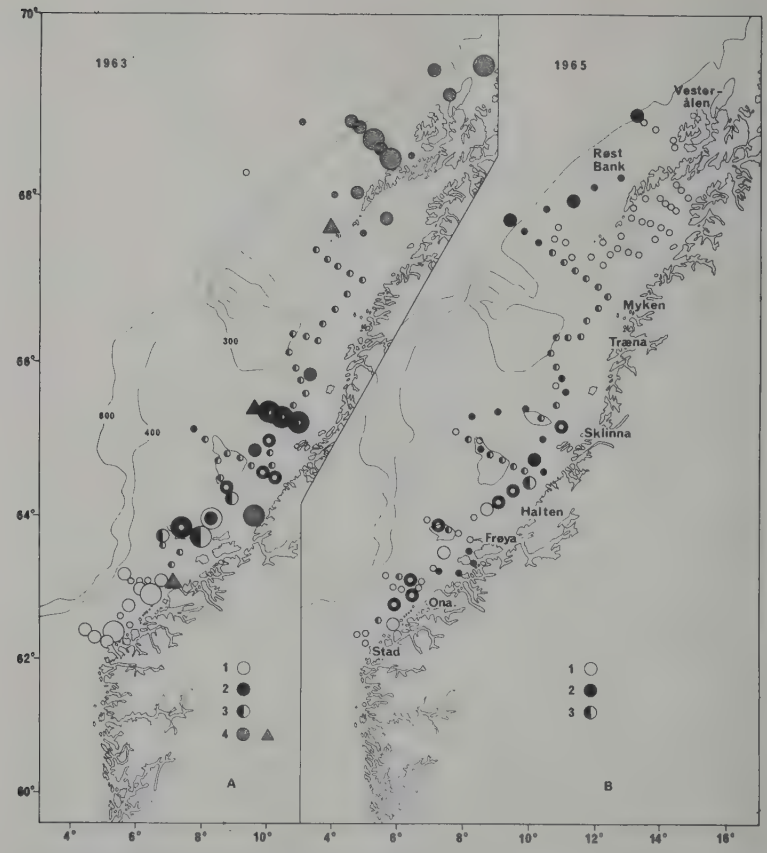

Fig. 4. Zooplankton volumes, ml/m² of sea surface.
A) 1963, 16—22 April. 1) CB, 50—0 m. 2) N 70, bottom—0 m. 3) Equal volumes in both gears. 4) J 36, 30 April—13 May. B) 1965. 1) J 80, bottom—0 m, 29 March—5 April. 2) J 36, bottom—0 m, 6—12 April. 3) Equal volumes in both periods. Symbol size as in Fig. 1.

Diurnal variations in the volumes of plankton in the upper 50 m were studied on the Frøya bank on 20—21 April, CB hauls being taken around drifting subsurface dragues (DRAGESUND and WIBORG 1963). The extremes were 27 ml/m² at 1400 hr and 82 ml/m² at 0800 hr (Tabel 1). The variations were probably caused both by vertical migration of the plankton and by shifting of water masses with varying contents of plankton. Similar

variations were observed in the numbers of herring larvae (DRAGESUND and WIBORG 1963).

During the first half of May maximum figures in vertical hauls were 200, 76 and 160 ml/m² off Ona, Frøya and Sklinna respectively.

Table 1. Volumes of plankton per m² of sea surface in the upper 50 m at a drift station on the Frøya bank 20—21 April 1963. CB hauls.

Hr	0800	1000	1200	1400	1600	1800	2000	2200	2400	0200	0400	0600	0800
ml/m²	82	68	66	27	33	65	38	44	31	31	48	30	53

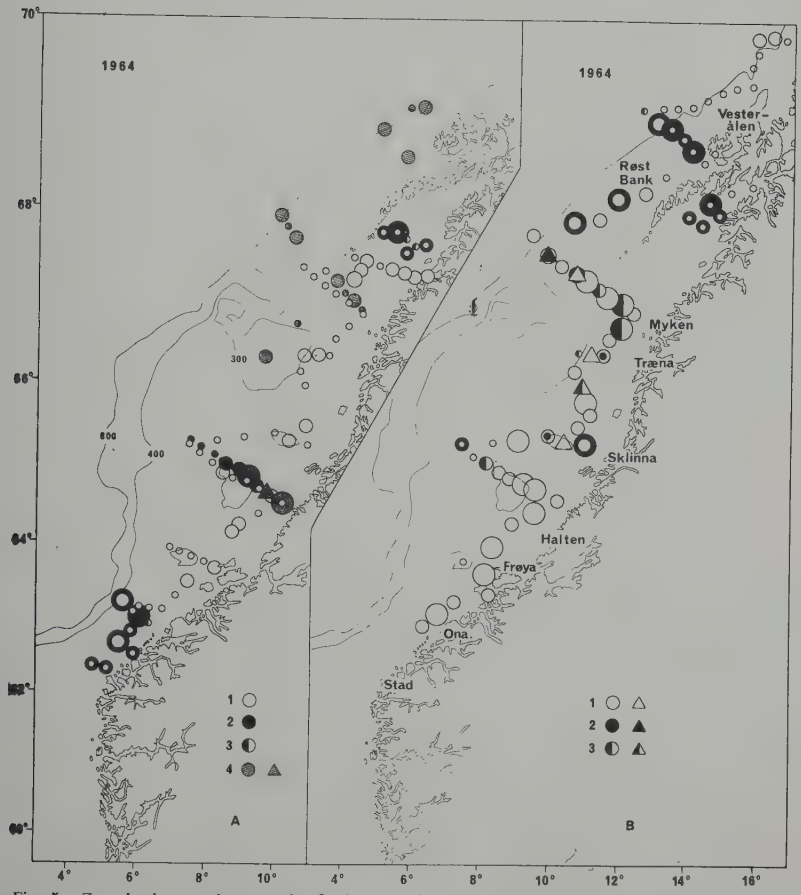

Fig. 5. Zooplankton volumes ml/m² of sea surface.
A) 1964. 1) CB, 50—0 m, 14—23 April. 2) J 36, bottom—0 m, 14—23 April. 3) Equal volumes in both gears. 4) CB, 50—0 m, 20—23 April. B) 1964, 23 April—5 May. 1) CB, 50—0 m. 2) J 80, bottom—0 m. 3) Equal volumes in both gears. Symbol size as in Fig. 1.

1964

(J 36 and J 80, bottom to 0 m, CB in the upper 50 m. Fig. 5.)

During the second half of April plankton was mostly scarce, as a rule less than 35 ml/m². *C.finmarchicus* stage IV copepodites predominated. A diurnal drift station on the Sklinna bank on 18 and 19 April (Table 2) yielded 19—32 ml/m² during the first 12 hours (1400 hr — 2400 hr) and 5—18 ml/m² from 0400 hr to 1400 hr. It is probable that different water masses were fished.

Table 2. Volumes of zooplankton per m² of sea surface in the upper 50 m at a drift station on the Sklinna bank 18—19 April 1964. CB hauls.

Hr	1400	1600	1800	2000	2200	2400	0200	0400	0600	0800	0900	1000	1200	1400
ml/m²	21	22	30	21	32	25	19	13	9	9	14	18	5	5

The Halten bank was visited twice at 6 days intervals, on 17 April and 23 April respectively. On the first date plankton was scarce, 5—25 ml/m², but the next time figures increased to 45—115 ml/m², and maximum concentrations went up to 4.0 ml/m³.

From 23 April to 2 May plankton was much more abundant than 10 days earlier, in some places more than 100 ml/m², and off Frøya 60—90 ml/m² and 1.5—3.0 ml/m³. The development of *C.finmarchicus* had progressed to equal proportions of copepodite stages IV and V.

At a drift station on the Røst bank 28—29 April plankton volumes varied between 11 and 68 ml/m², with a maximum at midnight (Table 3).

Table 3. Volumes of zooplankton per m² of sea surface in the upper 50 m at a drift station on the Røst bank 28—29 April 1964. CB hauls.

Hr	1000	1200	1300	1500	1700	1900	2100	2300	0100	0300	0500	0700	0900
ml/m²	12	11	23	21	33	51	63	68	33	24	19	24	22

At a drift station on the Træna bank on 30 April—1 May the volume variations were small and irregular, 33—65 ml/m² (Table 4).

Table 4. Volumes of zooplankton per m² of sea surface in the upper 50 m at a drift station on the Træna bank 30 April—1 May 1964. CB hauls.

Hr	2200	2400	0100	0300	0600	0800	1000	1300
ml/m²	65	44	33	39	35	63	41	43

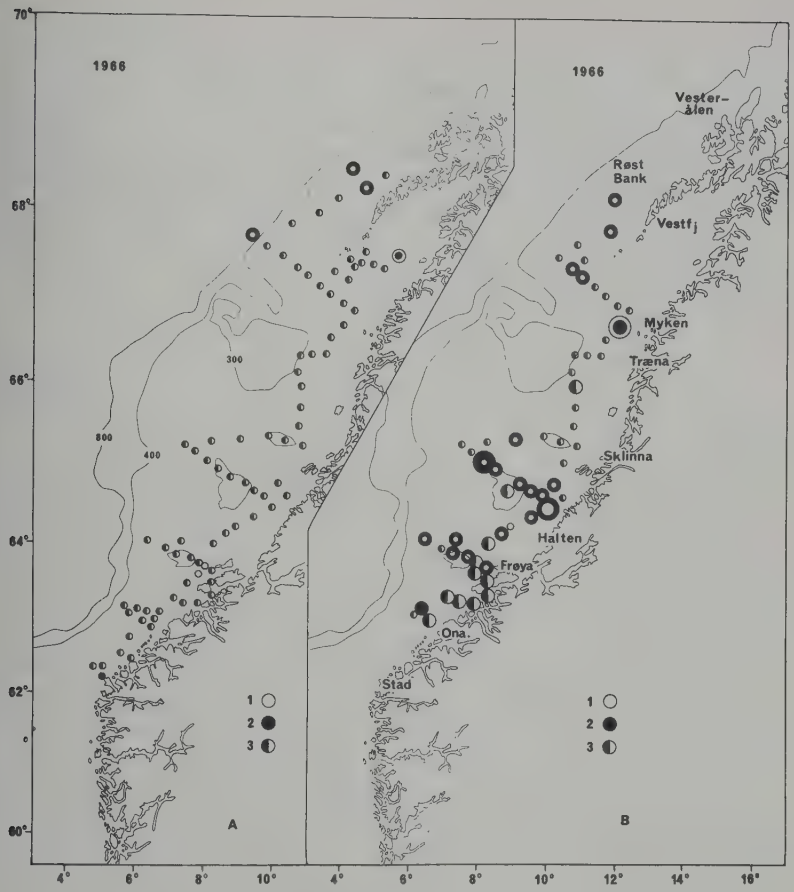

Fig. 6. Zooplankton volumes, ml/m³ of sea surface.
A) 1966, 15—23 April. 1) CB, 50—0 m. 2) J 36, bottom—0 m. 3) Equal volumes in both gears. B) 1966, 23 April— 5 May. 1) CB, 50—0 m. 2) J 80, bottom— 0 m. 3) Equal volumes in both gears. Symbol size as in Fig. 1.

1965

(J 36, J 80, bottom to 0 m. Fig. 4 B.)

During the period 28 March—12 April the coast and bank areas were surveyed twice. Plankton was scarce, less than 10 ml/m² in the CB hauls, and maximum 40 ml/m² in the vertical hauls. Stage IV—V copepodites and females of *C.finmarchicus* predominated, indicating an early spring situation.

1966

(J 36, J 80, bottom to 0 m, CB in the upper 50 m. Fig. 6.)

Plankton hauls were taken from 15 April to May. At the beginning of the period plankton volumes were mostly below 10 ml/m² with maxima of 20 ml/m² in the vertical hauls. *C.finmarchicus* stage II—III copepodites predominated. At the end of the period volumes had increased in the Ona—Halten area to 46—60 ml/m² in vertical hauls in which copepodites of stage IV predominated. Farther north plankton was scarce and *C.finmarchicus* was still in stages II—III.

DISCUSSION

In the coastal area off western and nortwestern Norway the maximum in zooplankton biomass is usually reached during May though sometimes in the northernmost area not until June (WIBORG 1954). In the eastern Norwegian Sea maximum usually occurs in June, later than on the coastal banks (PAVSHTIKS 1956, WIBORG 1954, 1955). However, conditions may vary from one year to another. In the area of the Norwegian current the dominant species, *C.finmarchicus,* started spawning in March in 1954, one month earlier than in 1951 (PAVSHTIKS 1956). The conditions in the open sea however, do not always correspond with those on the banks.

In the present investigation the material was collected mainly during April, and the biomass may not have reached the maximum. Some conclusions may nevertheless be drawn on the development of zooplankton during April—June. Average figures for the different areas are shown in Fig. 7 and Table I.

FIRST HALF OF APRIL

Plankton is generally scarce on the coastal banks, on an average 10 ml/m² or less, maximum 25—45 ml/m². Prespawning concentrations of *C.finmarchicus* may occasionally yield up to 90—110 ml/m² and 3.4 ml/m³ in the Stad—Frøya area.

SECOND HALF OF APRIL—BEGINNING OF MAY

Plankton is more abundant but figures vary considerably, averaging mostly 25—50 ml/m², maximum volumes in all areas 100—200 ml/m² and maximum concentrations 4—7 ml/m³. The large variations in abundance

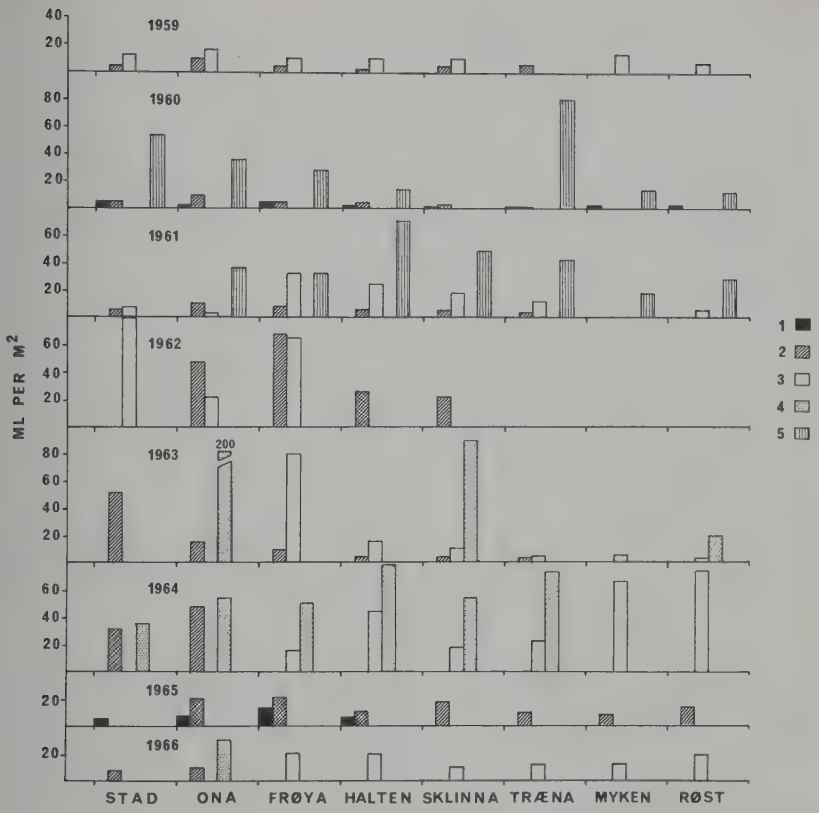

Fig. 7. Zooplankton volumes, ml/m² of sea surface. Average figures.
1) end of March, 2) first half of April, 3) second half of April, 4) first half of May, 5) second half of May — beginning of June.

may partly be caused by the varied vertical distribution of the plankton. According to TIMOKHINA (1964) zooplankton on the coastal banks in May is more evenly distributed in the upper 100 m and in June mainly in the upper 50 m.

MIDDLE OF MAY

Observations from one year only; with volumes of 75—200 ml/m² in the Ona—Sklinna area.

END OF MAY – BEGINNING OF JUNE

Average volumes are slightly higher than in April, 30—60 ml/m², and maximum volumes and concentrations are of about the same magnitude as in late April.

Observations from earlier years may be used for comparison. During May—June 1949—1951 the quantitative distribution of zooplankton was studied off northern Norway in the Lofoten—Vesterålen area (WIBORG 1954). At the beginning of May 1951 volumes of 50—100 ml/m² were recorded over relatively wide areas. At the beginning of June the figures increased even more, some areas with more than 100 ml/m², maximum 190 ml/m² and concentrations of 6.0 ml/m³.

In the middle of June 1974 the average volume on the Røst bank was 44 ml/m², in the Vestfjord 36 ml/m², maximum 106 ml/m²; in the middle of June 1975 the corresponding figures were 39, 39 and 255 ml/m² respectively; in the Ona—Stad area the average volume in the middle of June 1975 was 42—51 ml/m², maximum 110 ml/m² (WIBORG, unpublished).

(The samples taken in June 1974 and 1975 were measured fresh, and in order to compare the volumes with those of preserved samples, the figures have been reduced to 85% as indicated for copepod plankton by AHLSTROM and THRAILKILL (1963).)

In a section along 67°30' N. TIMOKHINA (1965) estimated the average quantity of zooplankton in Norwegian coastal waters (Røst Bank) in May to be 61.3 g/m² (= ml/m²). Large quantities have been recorded in June, sometimes more than 100 g/m² (TIMOKHINA 1972) and even 220 g/m² (4476 mg/m³ in the upper 50 m, (NESTEROVA 1974), mainly consisting of *C.finmarchicus* stage IV—V.

The areas of maximum abundance seem to vary from one year to another and also from season to season. The patchy occurrence of the plankton is indicated by great differences in volumes at stations situated close to each other, or in hauls taken at short intervals at the drift stations. Rich plankton patches are very often found on or close to the edge of the continental shelf, and on and around the banks.

Some calculations have been made of the total biomass of zooplankton on the coastal banks between Stad and Vesterålen (see Fig. 6), a distance of about 900 km. Assuming an average continental shelf width of 150 km, the area will be approximately 135 000 km². With an average volume of plankton at the beginning of June of 50 g/m² or 50 t/km², the total biomass will be about 6.8×10^6 t. If similar conditions prevailed along the remainder of the Norwegian coast, about 1 200 km in length, in a zone averaging 100 km in width, or 120 000 km², the biomass of zooplankton in this area would be $120\,000 \times 50 = 6 \times 10^6$ t.

TIMOKHINA (1964) found that in May—June 1959 *C.finmarchicus* constituted 80—90% of the total plankton biomass in Norwegian coastal waters. She calculated the annual production of *C.finmarchicus* in this area to be about 103 t/km^3. Applying this figure to the Stad—Vesterålen area we obtain: $103 \times 135\,000 = 13.9 \times 10^6$ t, and for the remaining coastal areas: $103 \times 120\,000 = 12.4 \times 10^6$ t, in total: 26.3×10^6 t/year.

The average primary production in coastal areas is assumed to be in the order of 100 t C/km^2/year (RYTHER 1969). If this figure is applied to the Norwegian coastal areas the annual primary production should be $(135\,000 + 120\,000) \times 100 = 25.5 \times 10^6$ t C. Assuming further an ecological efficiency factor of 10—20% and 10% of C in the wet weight of zooplankton (RYTHER 1969), the annual secondary production of zooplankton along the coast of Norway would be of an order of $26—52 \times 10^6$ t. This is quite close to be above figure of 26.3×10^6 t/year based on calculations by TIMOKHINA (1964)

If calculations are continued to the next link in the food chain, the annual production in the Norwegian coastal areas of fish, mammals and other organisms feeding on zooplankton will be of an order of 2.5—10 x 10^6t.

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Table I. Quantitative distribution of zooplankton off western and northwestern Norway in March—June 1959—1966. For gear symbols — see text.

Area	Year	Date	Gear	No. of st.	ml/m² sea surf.			ml/m³	C.finm. dom. stage
					aver-age	min.	max.	max.	
Stad	1959	5. IV	N 70	7	4.0	1.3	7.5		
		27. IV	0/100	5	13.8	5.0	37.5		
Ona		7–8. IV	0/100	14	9.7	1.8	41.5		
		26. IV	0/100	7	17.7	3.8	42.5		
Frøya		8–9. IV	0/100	7	3.8	0.6	12.5		
		25. IV	0/100	8	10.1	1.2	15.6		
Halten		10–11. IV	0/100	8	2.8	0.6	8.8		
		24–25. IV	0/100	5	9.2	6.3	10.6		
Sklinna		13. IV	0/100	5	3.9	0.6	6.3		
		24. IV	0/100	3	9.6	5.0	12.5		
Træna		13–14. IV	0/100	11	5.6	0.6	29.5		
Myken		22–23. IV	0/100	7	15.0	6.3	50.0		
Røst		19–20. IV	0/100	7	6.3	2.5	14.4		
Stad	1960	22. III	N 70	6	4.3	1.5	5.0		
		7. IV	N 70	3	4.3	4.0	5.0		
		24. V	CB	4	52.9	9.8	83.5	2.1	
Ona		23. III	N 70	7	2.8	1.5	4.0		
		5. IV	N 70	5	10.0	5.0	18.0		
		27. V	CB	7	36.1	21.5	85.5	2.9	
Frøya		23. III	N 70	8	5.4	1.5	10.0		
		4. IV	N 70	5	4.7	1.5	8.0		
		27–28. V	CB	7	27.1	15.5	51.8	1.7	
Halten		24–25. III	N 70	9	2.7	1.5	8.0		
		4. IV	N 70	8	4.6	3.0	10.0		
		28–29. V	CB	5	14.3	6.8	25.3	0.7	
Sklinna		25. III	N 70	4	1.9	1.5	3.0		
		3. IV	N 70	4	2.8	1.5	3.0		
Træna		26. III	N 70	8	2.1	1.5	4.0		
		2. IV	N 70	7	2.3	1.5	5.0		
		29–30. V	CB	4	79.4	42.0	177.3	6.6	
Myken		28. III	N 70	8	1.5	1.5	1.5		
		30. V	CB	10	14.0	6.8	19.8	0.6	
Røst	1960	29–30. III	N 70	11	2.7	1.5	8.0		
		8–9. VI	CB	15	12.5	1.0	39.3	1.4	
Stad	1961	10. IV	J 36	6	4.3	1.5	5.0		
			CB	6	3.0	0.5	4.3		
		29. IV	N 70	6	6.2	3.8	20.0		
Ona		11. IV	J 36	5	9.6	4.0	12.0		
			CB	8	5.3	1.6	10.5		
		28. IV	J 36	4	2.3	11.4	15.4		
		29. V	CB	7	37.1	11.3	100.8	3.7	

Table I. (cont.)

Area	Year	Date	Gear	No. of st.	ml/m² sea surf.			ml/m³	C.finm. dom. stage
					aver-age	min.	max.	max.	
Frøya		12. IV	J 36	5	7.2	4.0	8.0		
			CB	7	4.0	2.9	5.7		
		27. IV	J 36	5	32.0	16.0	40.0		
			CB	4	10.1	3.9	25.4		
		29–30. V	CB	5	33.4	18.5	65.5	2.6	
Halten		12. IV	J 36	7	5.1	4.0	8.0		
			CB	9	2.2	0.8	4.6		
		26. IV	J 36	8	24.8	12.0	48.0		
			CB	8	2.8	0.8	4.4		
		30–31. V	CB	7	71.7	20.3	146.8	5.2	
Sklinna		13. IV	J 36	5	3.5	0.5	8.0		
			CB	5	2.4	0.9	4.0		
		25. IV	J 36	5	18.0	10.5	28.0		
			CB	5	5.9	2.6	10.3		
		31. V	CB	4	49.8	31.5	76.3	2.5	
Træna		14. IV	J 36	8	4.3	0.5	20.0		
			CB	5	3.4	2.5	4.7		
		24. IV	J 36	5	12.8	4.0	16.0		
			CB	3	2.2	0.7	3.8		
		30. V	CB	6	42.9	16.3	95.5	2.7	
Myken		1. VI	CB	10	18.2	10.8	22.5	0.7	
Røst		20–21. IV	CB	13	3.0	0.6	4.2		
		2–3. VI	CB	11	28.1	5.3	60.8	2.0	
Stad	1962	25. IV	J 36	5	70.5	16.0	112.0		
			CB	5	80.3	20.3	179.5	7.1	
Ona	1962	4. IV	J 36	6	43.3	16.0	88.0		
			CB	6	24.9	14.5	42.0	1.4	
		11–12. IV	J 36	6	47.3	20.0	92.0		
			CB	6	8.9	4.3	15.8	0.6	
		26. IV	CB	6	22.3	5.8	59.3	2.3	
Frøya		5. IV	J 36	5	28.0	20.0	40.0		
			CB	5	10.8	1.5	22.0	0.4	
		10. IV	J 36	5	68.0	48.0	02.0		
			CB	5	14.6	7.3	23.0	0.7	
		26–27. IV	J 36	5	65.6	24.0	96.0		
			CB	5	74.0	56.3	117.5	4.0	
Halten		5–6. IV	J 36	8	10.5	4.0	24.0		
		10. IV	J 36	7	26.8	4.0	44.0		
			CB	7	2.4	1.5	4.0		
Sklinna		5–6. IV	J 36	4	22.0	16.0	32.0		
Stad	1963	2–3. IV	N 70	5	5.0	1.3	12.5		
		8. IV	CB	3	52.5	18.8	109.3	3.4	

Table I. (cont.)

Area	Year	Date	Gear	No. of st.	ml/m² sea surf.			ml/m³	C.finm. dom. stage
					aver-age	min.	max.	max.	
Ona		8. IV	J 80	1	16.0	—	—		
			CB	2	16.5	2.0	31.0		
		13. V	J 36	1	200.0	—	—		
Frøya		3. IV	N 70	6	2.5	0.5	6.3		
		6–7. IV	N 70	5	10.0	5.0	17.5		
		21. IV	N 70	4	79.3	62.5	102.3		
			CB	4	38.6	12.0	82.3	2.5	
Halten		3. IV	N 70	10	0.8	0.5	2.5		
		7. IV	N 70	6	2.9	1.3	6.3		
		19. IV	N 70	10	16.3	1.3	5.0		
			CB	10	6.6	15.0	19.5		
Sklinna		6–8. IV	N 70	5	2.3	1.3	5.0		
		17–18. IV	N 70	5	11.3	7.5	16.3		
			CB	5	4.6	2.3	7.0		
		10. V	J 36	4	90.0	58.0	160.0		
Træna		8. IV	N 70	5	2.0	0.5	2.5		
		17. IV	N 70	4	1.3	0.5	7.5		
Træna	1963	17. IV	CB	5	2.7	1.7	6.3		
Myken		16–17. IV	N 70	7	5.4	2.5	15.0		
			CB	7	3.3	2.0	4.5		
Røst		15–16. IV	N 70	12	2.5	1.3	15.0		
		8. V	J 36	6	21.3	4.0	32.0		III–IV
Stad	1964	14. IV	J 80	3	33.7	31.0	36.0		IV
			CB	3	9.3	5.3	15.3	0.4	
		5. V	CB	1	36.5	—	—	1.1	IV–V
Ona		15. IV	J 80	4	48.3	5.0	84.0		IV
			CB	7	13.0	4.5	24.5	0.7	
		4. V	CB	1	55.0	—	—	1.9	IV–V
Frøya		16. IV	CB	5	15.5	6.5	33.0	1.1	III–IV
		3. V.	CB	3	50.4	9.5	71.3	3.2	IV–V
Halten		17. IV	CB	10	16.4	5.8	24.3	0.8	IV
		23. IV	CB	8	45.7	11.0	112.5	4.2	
		2–3. V	J 80	4	79.0	30.0	188.0		IV–V
			CB	9	33.8	10.0	67.5	2.5	
Sklinna		17. IV	CB	4	17.7	6.3	33.0	0.9	IV
		2. V	J 80	2	55.5	11.0	100.0		IV–V
			CB	5	51.4	27.0	123.3	4.8	
Træna		19–20. IV	CB	5	21.7	17.0	28.0	0.7	IV
		1. V	J 80	3	73.0	10.0	198.0		IV
			CB	5	58.2	24.5	121.5	4.9	
Myken		20. IV	CB	6	13.7	9.5	21.0	0.5	IV
		21–22. IV	CB	7	21.0	8.5	31.5	1.0	IV
		30. IV	J 80	4	67.0	34.0	128.0		
			CB	9	54.2	13.8	113.3	4.0	IV–V

Table I. (cont.)

Area	Year	Date	Gear	No. of st.	ml/m² sea surf.			ml/m³	C.finm. dom. stage
					aver-age	min.	max.	max.	
Røst		27–28. IV	CB	12	12.5	7.3	24.0		IV–V
		29. IV	J 80	3	74.0	36.0	98.0		
			CB	4	37.6	25.0	61.0	1.7	
Stad	1965	29–30. III	J 80	3	7.0	6.0	8.0		
Ona		30. III	J 80	7	8.6	6.0	18.0		♀
		11–12. IV	J 36	3	21.3	4.0	32.0		♀
Frøya	1965	31. III	J 80	5	14.8	3.0	20.0		♀
		10–11. IV	J 36	2	22.0	20.0	24.0		♀
Halten		31. III–1. IV	J 80	9	6.8	1.0	24.0		IV–♀
		8. IV	J 36	11	11.3	4.0	28.0		IV–♀
Sklinna		2. IV	J 80	3	3.8	2.8	4.8		V–♀
		8. IV	J 36	2	16.0	12.0	20.0		V–♀
Træna		2. IV	J 80	5	2.0	1.0	3.0		V–♀
		7. IV	J 36	5	10.4	4.0	16.0		♀
Myken		2–3.IV	J 80	10	5.0	2.0	9.0		♀
		6–7. IV	J 36	9	9.8	8.0	24.0		♀
Røst		5–6. IV	J 80	9	14.8	4.0	40.0		♀
Stad	1966	15. IV	J 80	3	8.3	4.0	12.0		III
			CB	2	5.0	3.6	6.6		
Ona		15. IV	J 80	7	8.7	5.0	12.0		III
			CB	7	8.8	5.5	12.5		
		I. V	J 80	3	29.3	12.0	48.0		
		I. V	CB	2	17.5	7.0	28.0	0.8	IV
Frøya		16–17. IV	J 80	6	6.3	2.0	14.0		♀–III
			CB	8	4.6	3.5	7.5		
		27–28. IV	J 36	8	35.0	16.0	48.0		IV
			CB	7	16.9	12.0	24.8		
Halten		17–18. IV	J 80	13	9.9	3.0	20.0		♀–III
			CB	13	7.3	3.0	14.5	0.4	
		25–26. IV	J 36	13	29.2	8.0	60.0		
			CB	13	13.7	4.0	32.5	1.2	IV–V
Sklinna		19. IV	J 80	2	11.0	9.0	13.0		♀II–III
			CB	2	3.8	2.8	4.8		
		24–25. IV	J 80	3	11.2	8.0	16.0		
			CB	3	11.1	10.3	12.0	0.3	II–III
Træna		19. IV	J 80	5	8.0	6.0	14.0		
			CB	5	4.3	1.3	7.3		
		24. IV	J 80	5	18.4	12.0	28.0		
			CB	5	12.9	6.3	24.8	0.6	II–III

Table I. (cont.)

Area	Year	Date	Gear	No. of st.	ml/m² sea surf.			ml/m³	C.finm. dom. stage
					aver-age	min.	max.	max.	
Myken	1966	20–22. IV	J 80	8	9.6	6.0	16.0		
				(9)	(17.7)		(83.0)		
			CB	9	8.5	4.0	11.5	0.3	II–III ♀
		23–24. IV	J 80	7	15.4	4.0	36.0		
			CB	7	13.5	5.8	17.0	0.4	(♀) II–III
Røst		22. IV	J 80	5	15.4	4.0	28.0		
			CB	5	8.7	4.3	10.8	0.3	
		23. IV	J 80	5	23.2	12.0	32.0		
			CB	5	8.7	3.8	12.5	0.2	

FiskDir. Skr. Ser. HavUnders., *16*: 279—300.

STUDIES ON THE LONG TERM STORAGE OF LIVING SAITHE, *Pollachius virens* Linnaeus, 1758*

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ABSTRACT

Bratland, P., Krishnan, S. and Sundnes, G. 1976. Studies on the long term storage of living saithe, *Pollachius virens* Linnaeus, 1758. *FiskDir. Skr. Ser. HavUnders.*, 16: 279—300.

In order to observe how far muscle nutrition is affected during long term starvation, saithe were stored under natural and laboratory conditions. The results show that changes in the liver and condition indices were similar under both conditions. The analyses of protein, water, lipids, carbohydrates and ash content indicate that in the white muscle there is a loss of protein during starvation. The protein loss is replaced by water. Such a correlation was not found in red mucsle. There was no definite trend in carbohydrate and ash content of muscles with advance of starvation. The overall picture of the various chemical analyses shows that the organic material from white muscle is mobilised when the saithe are starved, whereas there is little change in the red muscle.

INTRODUCTION

Ever since the beginning of this century live saithe have been transported and stored and live animals have been sold on the domestic market. In recent years the annual catch of saithe has increased considerably and the fillet industry has grown to be one of the largest purchaser of live saithe.

The catch quantity of saithe fluctuates seasonally and these fluctuations affect the fillet industry's production. During the summer season the offer (supply) of saithe to the fillet industry is greater than the processing capacity. Therefore, in order to obtain an optimum use of the resource a buffer between the catching and the processing sectors is required. In practice, buffering is effected by storing the surplus quantity of saithe and

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using this surplus to supply the fillet industry during those periods when the catch level is lower than the industry's receiving capacity. It is of great importance, therefore, to store saithe efficiently during these times of large surplus catches either as frozen fish or as living fish held in seines.

One of the chief aims in developing an efficient storage technique is to keep the cost to a minimum. In this respect storage of living saithe has appreciable advantage over freezing, especially when the animals are stored without feeding. Such conditions do not impose unnatural stress as fish in the wild experience starvation in the course of natural cycles of food availability. In our latitudes fish usually have a good supply of food during the summer months while during the winter months they live chiefly on stored nutrition in the body tissues, especially the liver. It is this cycle which is desired to exploit. Under a well planned storage programme it should be possible to hold saithe in seines for periods of up to three months with little detriment to musculature, or in other words, the fillet.

It is normal to find that fish in poor condition have greater water content in the tissue than healthy fish (Love 1960, Johnston and Goldspink 1973). This cannot be registered by measurement of the fish's condition based on a length-weight relationship alone. For examphe, salmon migrating up-stream have the same conditon factor during the entire journey, however, protein is successively replaced by water as the fish swim up-river (Greene 1919, Parker and Vanstone 1966).

It was of interest to know whether a similar change in quality would occur in saithe during a complete absence of feeding.

The experiments described here were carried out to investigate biochemical changes in musculature of living saithe stored under various conditions.

MATERIALS AND METHODS

The experiments were performed on purse seine caught saithe.

The experimental conditions of storage in fjords and laboratory tanks with circulation of sea water of constant temperature and salinity were chosen to determine the effects of storage. Table 1 gives the details of experimental conditions. Fig. 1 shows the locations of the field experiments.

Ten samples were taken at intervals of ten days from the fjords (except at Lepsøy where samples were taken weekly), and in the laboratory experiments samples were taken each week. Samples from Leines and Sørøy were frozen for transportation. Samples from Lepsøy and from

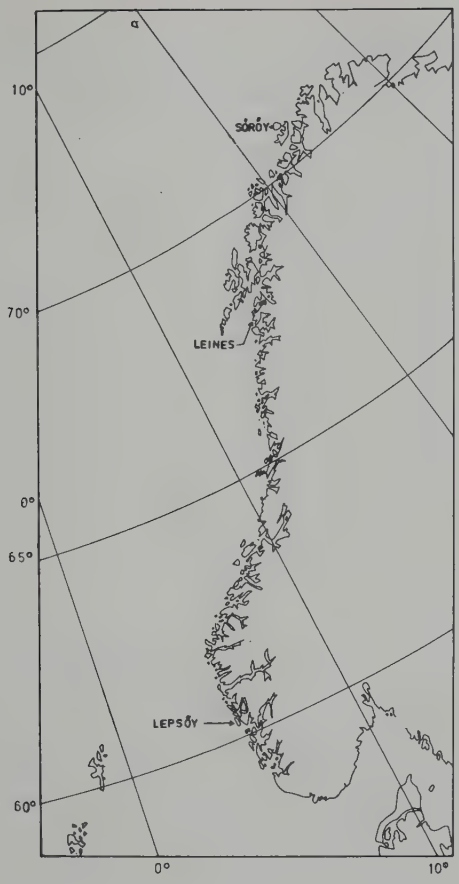

Fig. 1. Localities of saithe storing experiments.

the laboratory experiments were analysed fresh. In order to observe the rate of recovery after starvation the fish were fed for four weeks after twelve weeks of starvation in the lab. '74 set of experiments.

Pieces of muscle for the biochemical analyses were cut from the lateral side just above the ventral fin. Red and white muscles were analysed separately in samples from Sørøy fjord and from the lab. '74 experiment.

The water content was measured by weighing the samples before and after drying at 75°C in a hot air oven. Biochemical analyses were carried out on dry tissue samples.

Table 1. Storage conditions during the starvation experiments on saithe.

Locality and time of year	Storage time	Temperature range and mean temperature (°C)	Salinity (‰)	Quantity stored (Q) (Kg)	Seine volume (S) (m^3)	Density factor (Q/S)	Weight range and mean weight (g)
Lepsøy (Bergen) Winter	25 Nov 1972— 28 Feb 1973	7.2—4.7 6	31.00	500	100	5.00	300— 600 410
Leines (Bodø) Fall	15 Aug 1973— 11 May 1974	9.0—4.0 6.7	32.60	80.000	1.700	4.80	350— 700 470
Sørøy (Hammerfest) Fall		6.4—4.0 5.1	33.25	170.000	31.820	5.30	4000—2000 1550
Lab. exp. (Bergen) Spring		8.5	34.00	75	750*	10.00	300— 400 340
Lab. exp. (Bergen) Spring		8.5	34.00	350	3.500*	10.00	300—1100 700

* In case of laboratory experiments the volume of the tank was taken to calculate the density factor (Q/S).

The muscle samples were analysed for total protein, carbohydrate and lipid content. Protein was analysed either by the KJELDHAL or by the modified BIURET method (RAYMONT, AUSTIN and LINFORD 1964). Total sugars were estimated by the phenol-sulphuric acid method (DUBOIS *et al.* 1956). Total lipids were extracted using a mixture of methanolchloroform (RAYMONT *et al.* 1964). Ash was measured by burning the tissues in a muffle furnace at 600°C for ten to twelve hours.

The condition of the fish was measured in terms of liver index (L) where

$$L = \frac{\text{wet weight of liver}}{\text{wet weight of body}} \times 100,$$ and conditon index (C) where

$$C = \frac{\text{weight}}{\text{weight}^3} \times 1000.$$ The liver index was also compared with water, protein and lipid content of muscle. Water content of muscle was compared with the protein and lipid content, and protein was compared with lipids.

RESULTS

The data for the condition index show that there was slight decrease in condition in all fish except for those from Sørøy. These were in the best conditon at the beginning of the experiment as indicated by data for both condition index and liver index (Fig. 2 and 3). Liver index was directly correlated with conditon index except for Sørøy fish (Fig. 4).

In fish stored in the fjord at Sørøy and Lepsøy there was a negligible increase of water in the white muscle compared to the fish stored at Leines where there was heavy increase. Also in the laboratory experiments there was an increase of water in white muscle (Fig. 5). Red muscle on the other hand showed a decreasing water content during the experiment.

In three of the five experiments (i.e. lab. '73, lab. '74 and Leines) there was an inverse correlation between water content of white muscle and liver index (Fig. 6). This is also reflected when compared with condition index (Fig. 7).

Protein content of white muscle in fish stored in the fjords decreased by less than 1.5% during starvation, except for the fish from Leines (Fig. 8), where the decrease was highly pronounced. There was direct correlation between protein content of white muscle and liver index (Fig. 9) and between protein and water content (Fig. 10). The protein content of red muscle decreased during starvation in Sørøy fish, but increased in lab. '74 fish.

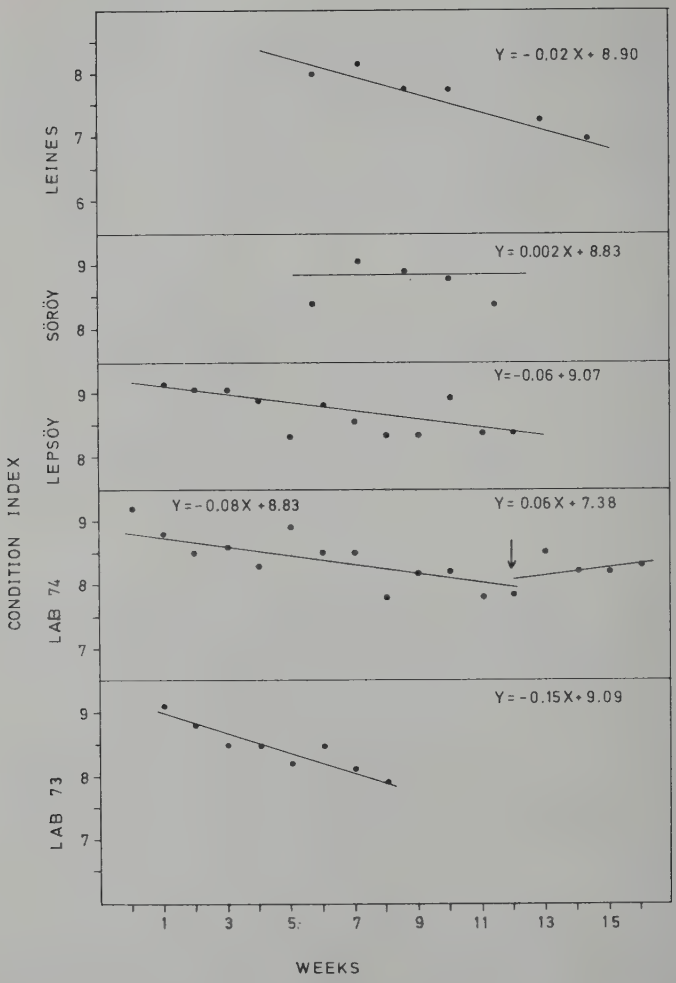

Fig. 2. Saithe condition index (C) during prolonged starvation. Arrow indicates the start of feeding.

Changes in carbohydrate content of white muscle did not show the same trend in all the experiments. There was a decrease in carbohydrate for fish from Leines and from the lab. '73 experiment, an increase in Sørøy fish and no significant change in fish from Lepsøy and in the lab. '74 experiment (Fig. 11).

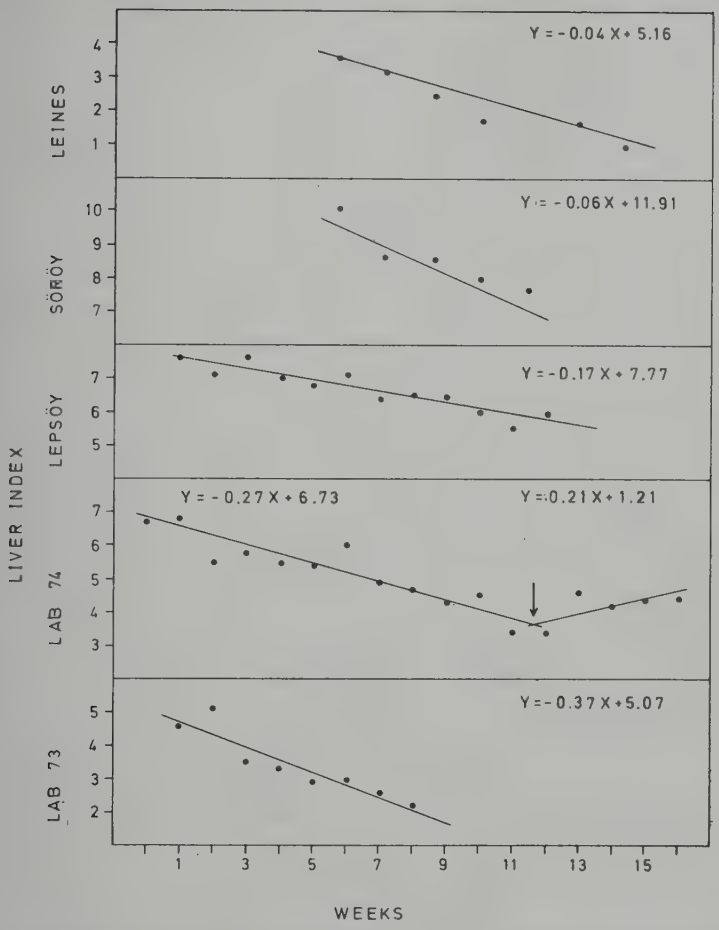

Fig. 3. Changes in liver index (L) during starvation. Arrow indicates the start of feeding.

Lipid content of both white and red muscles increased in all cases, except for white muscle lipid in fish from Sørøy and the lab. '74 experiment (Fig. 12). The precentage increase of lipid in red muscle was greater than for white muscle and was inversely correlated with water content (Fig. 13). An inverse correlation was observed when a comparative graph was made with liver index versus lipid in the case of red muscle and in the case of white muscle from Lepsøy fish (Fig. 14).

The ash content of the fish from Leines, Lepsøy and the lab. '73 experiment decreased during starvation. In the lab. '74 experiment there

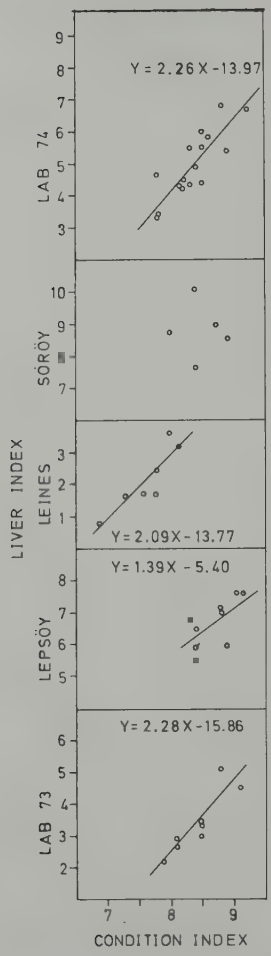

Fig. 4. Relationship between liver index and condition index.

was no significant change in percentage ash content of either red or white muscle during starvation, or when feeding was started after twelve weeks of starvation. In fish from Sørøy ash content of white muscle increased whereas ash content of red muscle decreased (Fig. 15.) Water content was inversely correlated with ash content only in the case of fish from Leines and the lab. '73 experiment (Fig. 16).

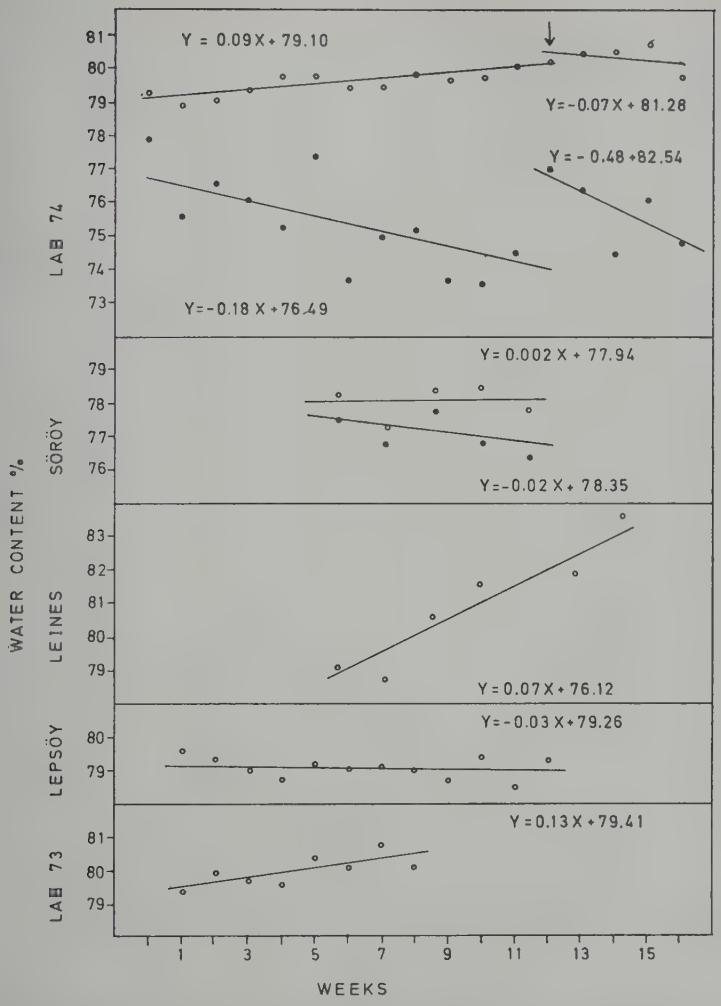

Fig. 5. Changes in water content of white (open circles) and red (solid circles) muscles. Arrow indicates the start of feeding.

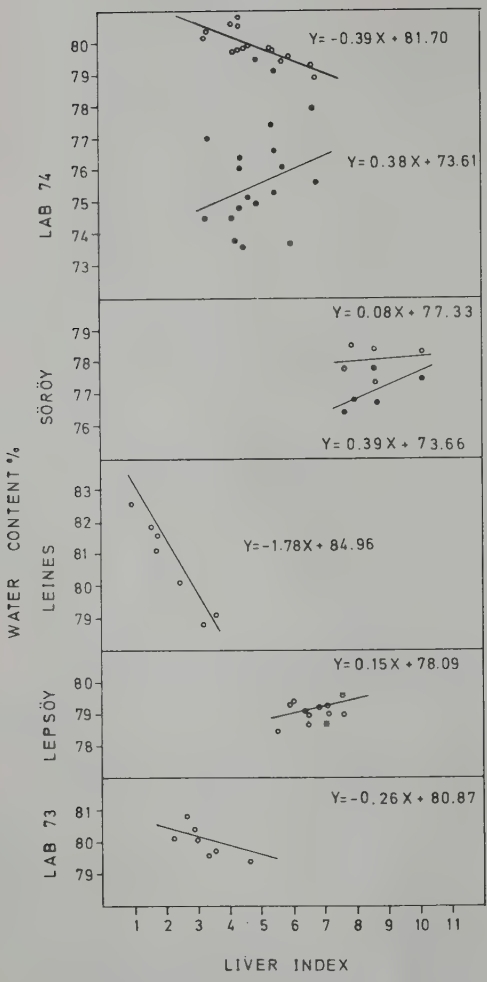

Fig. 6. Relationship between water content and liver index. White muscle: open circles; red muscle: solid circles.

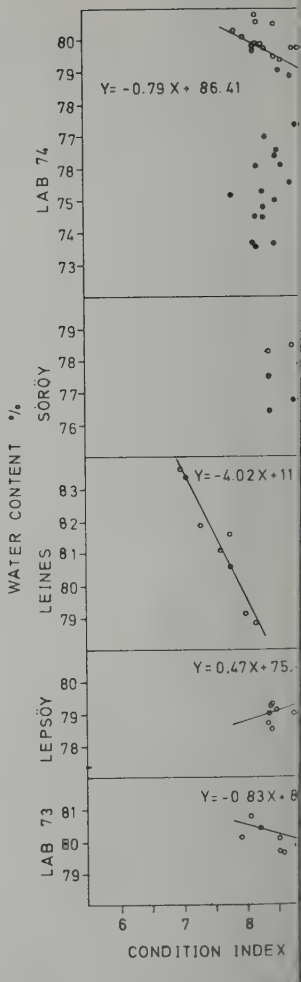

Fig. 7. Relationship betwe water content and condit index. White muscle: op circles; red muscle: solid circ

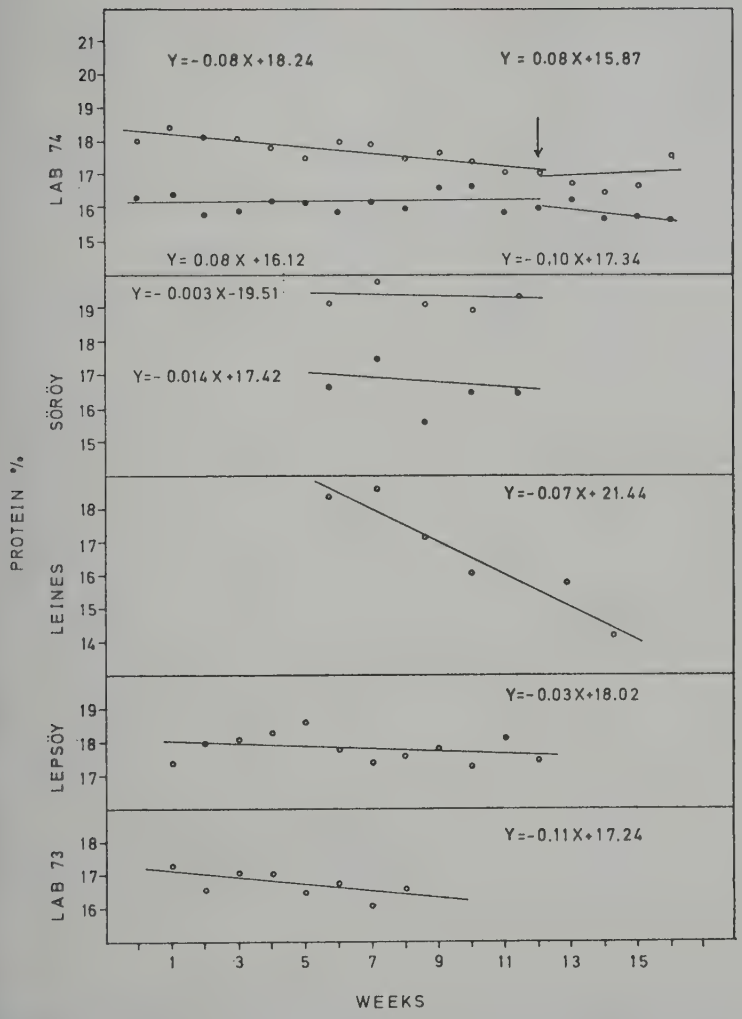

Fig. 8. Changes in total protein in white (open circles) and red (solid circles) muscles during starvation. Arrow indicates the start of feeding.

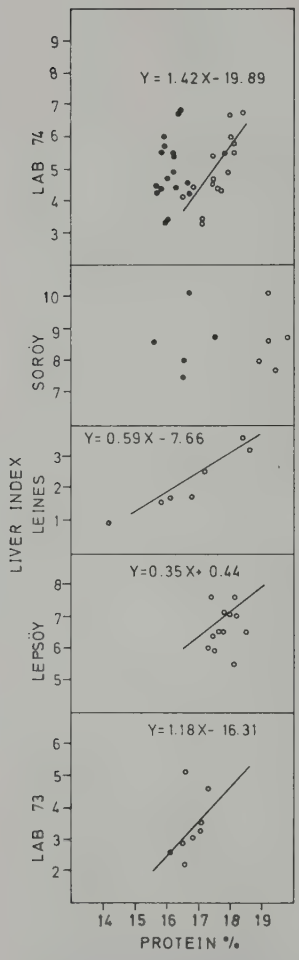

Fig. 9. Relationship between liver index and protein content in white (open circles) and red (solid circles) muscles during prolonged starvation.

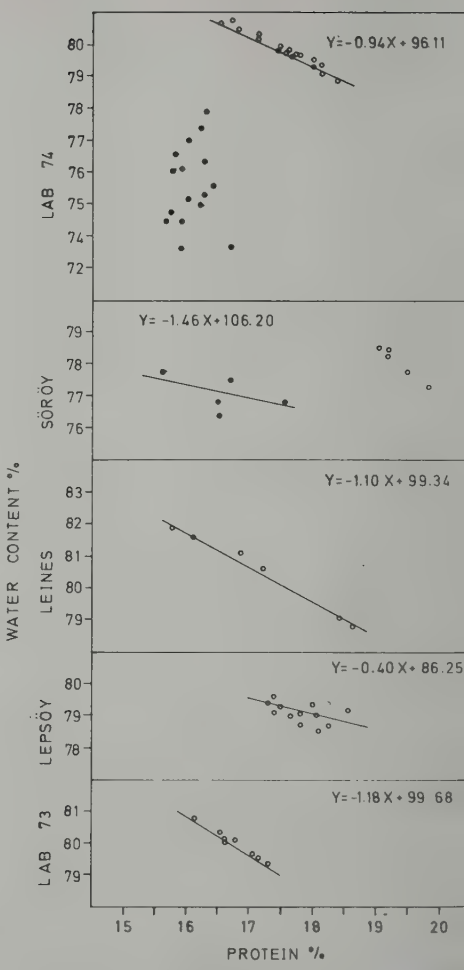

Fig. 10. Relationship between water content and total protein in white (open circles) and red (solid circles) muscles.

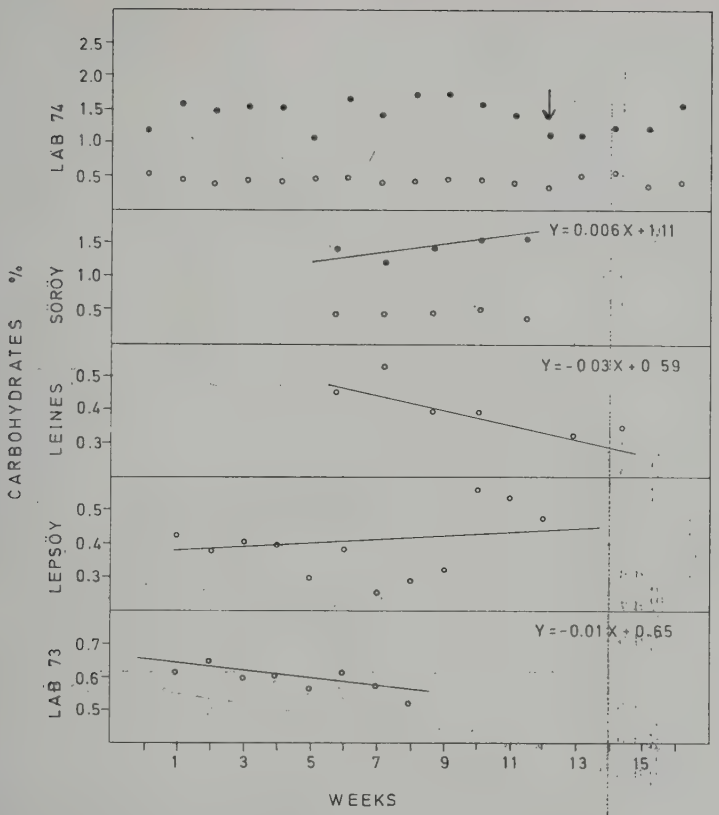

Fig. 11. Changes in carbohydrates in white (open circles) and red (solid circles) muscles during starvation. Arrow indicates the start of feeding.

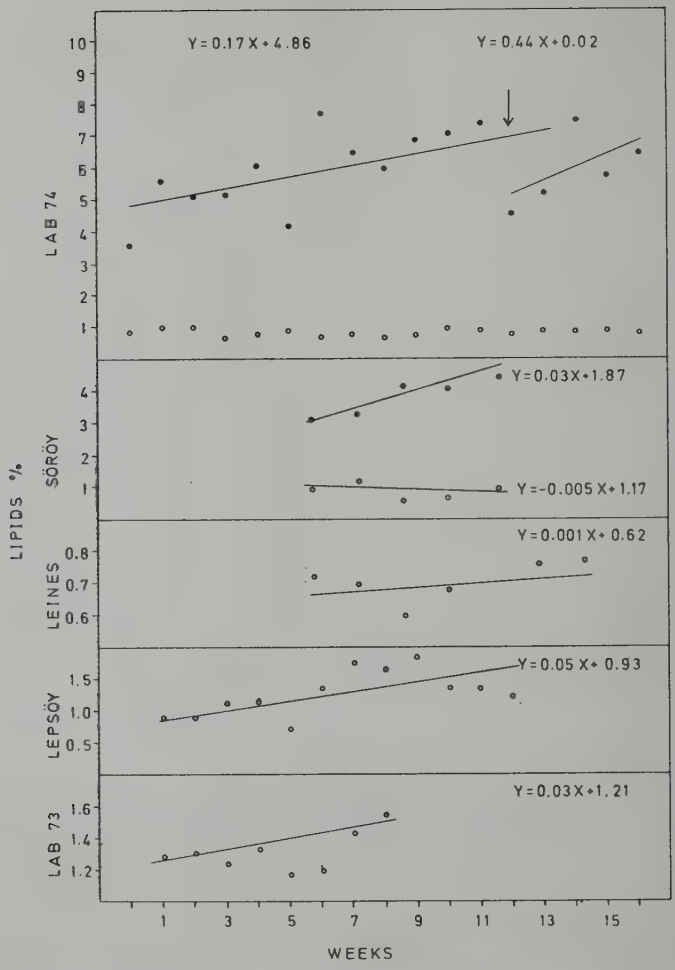

Fig. 12. Changes in lipid content of white (open circles) and red (solid circles) muscles during starvation. Arrow indicates the start of feeding.

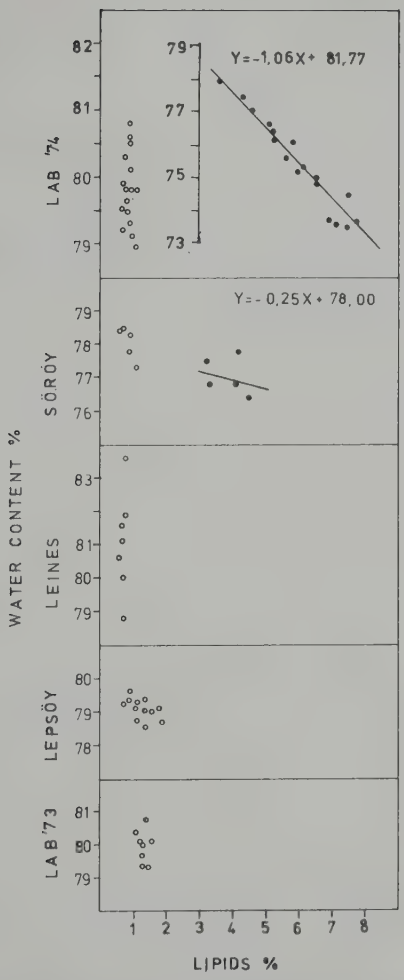

Fig. 13. Relationship between water content and lipids in white (open circles) and red (solid circles) muscles during long term storage.

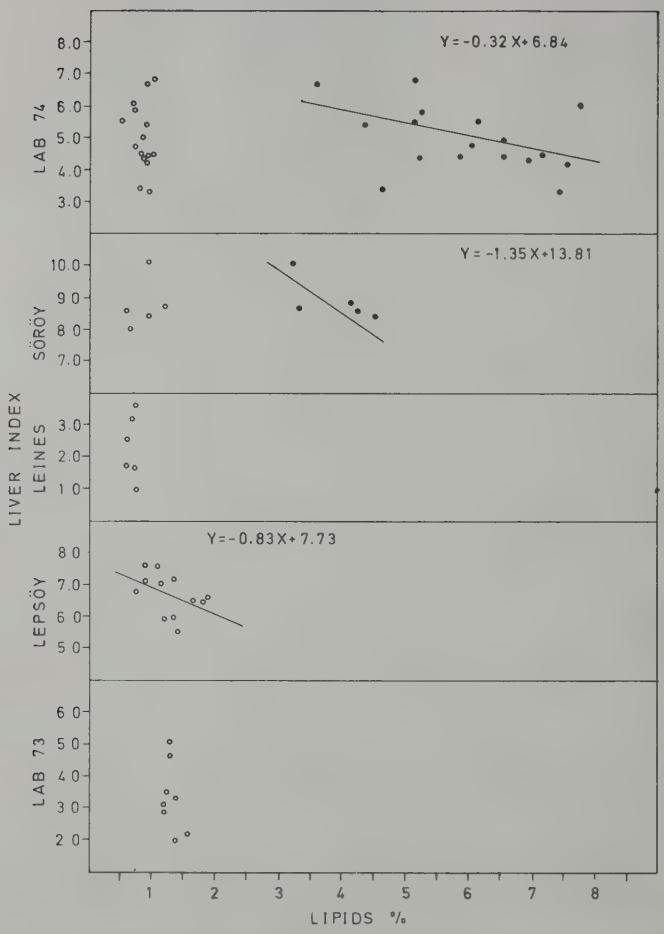

Fig. 14. Relationship of liver index and lipid content in white (open circles) and red (solid circles) muscles during starvation.

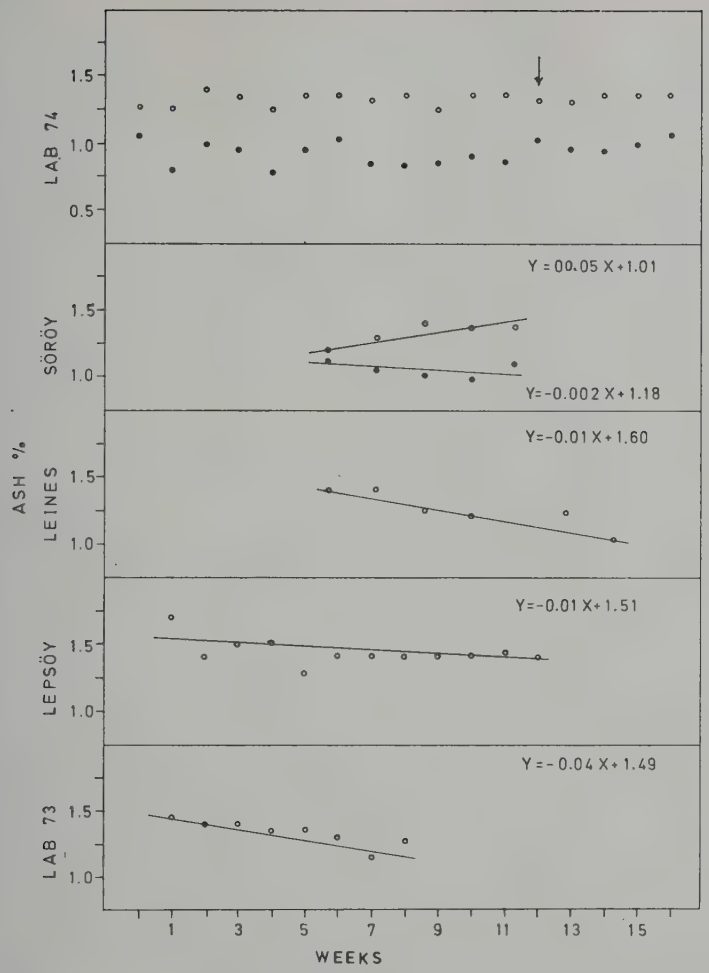

Fig. 15. Changes in ash content of white (open circles) and red (solid circles) muscles during starvation. Arrow indicates the start of feeding.

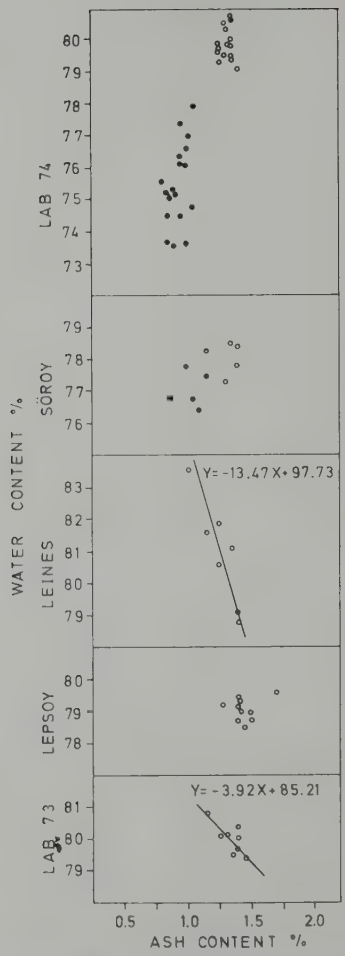

Fig. 16. Relationship between ash and water content in white (open circles) and red (solid circles) muscles during starvation.

DISCUSSION

These experiments on the prolonged starvation of saithe under natural and laboratory conditions have given diversified results. Considering the fish stored in fjords, there was a marked decline in the liver index in all three fjords. Fish stored at Sørøy had the highest liver index (8—10) at the start of the experiment, and in this group the rate of decline of liver index was greatest. This cannot be attributed to temperature since the mean temperature was the same (± 1°C) in all experiments. There was a similar decline in the liver index among fish held in the laboratory during summer 1973 and spring 1974, and this was slightly more marked in the summer. Even though the fish were fed after twelve weeks of starvation, after four weeks of feeding they still did not recover their original liver condition.

The change in condition index during starvation was similar in all fish except for those stored at Sørøy. This discrepancy in Sørøy fish may be due to sampling error in the first Sørøy sample. Both liver and condition indexes of fish in the lab. '74 experiment did not seem to reach the original level after four weeks of feeding.

The earlier works on fatty and non-fatty fish show that water content of muscle increases during starvation and migration. It has been reported by Idler and Binters (1959) that the water content of the muscle of sockeye salmon (*Onchorhynchus nerka*) increases by about 20% during up-stream migration. During starvation 86—88% water has been recorded in the muscle of the non-fatty fish cod (*Gadus morhua*) (Love 1958, Sutton 1968), and 96% water was reported in the muscle of *Hippoglossus platessoides* (Templeman and Andrews 1956). Compared to these values the increase of water in muscle tissue of saithe during starvation is less than the levels reported previously for non-fatty fish. In normal saithe the water content ranges from 78—82%, in these experiments it rose by only 2—4%. The water content seemed to be steady only in the Lepsøy stock of fish. This may be due to a low water temperature prevailing in that region (6°C) during the experimentation period or the metabolic rate of the fish being at a minimum. Due to the latter, the requirement for mobilization of protein from the muscle would have been less and hence the increase of water would appear to be small.

The analyses of red muscle showed a decrease in water content of 2—4%. This result is not in agreement with findings of Johnstone and Goldspink (1973), who reported an increase in the water content of red muscles of plaice (*Pleuronectes platessa*) during starvation.

Reviewing the changes in the chemical constituents of fish during starvation and migration, Love (1970) states that the impact of starvation

is felt sooner in active than in sluggish fish. Such an effect is seen in saithe which are active fish. In the experiments in Leines fjord the protein level fell by 4.5% wet flesh. The protein content decreased from 18.5% to 14.0%. A rapid decline in protein was also recorded in the laboratory fish experiments. The reason for the rapid decline in the laboratory fish protein may be the higher mean temperature in the laboratory experiments which probably resulted in a higher metabolic rate. The rapid decline in protein content of the fish stored at Leines may be due to the fact that these fish were smaller in size than those stored at Sørøy and Lepsøy, and therefore the metabolic rate per unit weight could have been higher than in the larger fish, and depletion of reserves would therefore be more rapid.

The main conclusion is that the low liver index at the beginning of the experiment in Leines fjord indicated that these fish were unsuitable for storage (Bratland, Krishnan and Sundnes 1974). The liver is the energy resource to a certain level beyond which the depletion of the muscular tissue increases.

A correlation was also observed between white muscle protein and liver index though no such correlation was found for red muscle. In the Sørøy fish the results were similar to those for white muscle, whereas in the laboratory experiments the trends were in reverse. The reason may be that protein is not released from red muscle during starvation. This was observed by Johnston and Goldpink (1973) on plaice. A protein-water relationship was found only in the red muscle of the Sørøy stock, but the liver index-red muscle relationship of this stock was found in neither group. In general there seems to be a good protein-water relationship for both the types of muscle. This observation agrees with that of Love (1970).

There was no significant change in carbohydrate content of red or white muscle during starvation, which indicates that the carbohydrates in the muscle tissue of saithe do not serve as a source of energy during starvation. Similarly, the results for lipid content show that muscle lipid is not mobilized during starvation.

The fact that cod, as stated by Love (1970) utilize liver lipids during starvation could also refer to saithe. Even though a higher quantity of lipids was recorded in the red muscle, the amount did not seem to decrease with advancing starvation. However, a good fat-water relationship was observed for the red muscle. There were inverse relationships for which no explanations were found between liver index and lipid in the red muscle and between liver index and lipid in white muscle of the Sørøy fish.

From chemical analyses carried out on red and white muscles it becomes obvious that the former contribute less organic material during

starvation than the latter. WALKER (1971), working on the effect of starvation on the skeletal muscle fibres of cod (*Gadus morhua*) and saithe (*Gadus Pollachius virens*), concluded that "during such periods or at times of food shortage, it is the white fibres that atrophy, the red fibres remaining nearly intact". This view has been supported by JOHNSTON and GOLDSPINK (1973). ROBERTS (1969) and PRITCHARD, HUNTER and LASKER (1971) have shown in dogfish (*Scyliorhinus canicula*) and in mackerel (*Symmetricus sp.*) respectively that the red muscle is used almost continuously for locomotor activity while the white muscle is used only for high speed swimming. Hence under captivity little use would be made of the white, tissue and mobilization of material from this tissue could be expected during starvation.

It has been reported for various species that ash content of muscle tissue falls as water content increases during starvation; TILLIK (1932) reported this in Atlantic salmon (*Salmo salar*), and KORDYL (1951) gave a similar result for cod (*Gadus morhua*). There was a similar decrease in ash content with the advance of starvation in three of the five experiments described here (Leines, Lepsøy and lab.'73). However, an ash-water correlation was not found in all groups (Fig. 15).

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ON THE RELATION BETWEEN ECHO INTENSITY AND FISH DENSITY

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ABSTRACT

Røttingen, I. 1976. On the relation between echo intensity and fish density. *FiskDir. Skr.Ser.HavUnders.*, *16*: 301—314.

Integrated echo intensities for a wide range of fish densities were measured. The experiments were carried out on live saithe (*Pollachius virens*) and sprat (*Sprattus sprattus*) which were kept in a net cage. Echo intensities were measured at 38 kHz and 120 kHz and pulse lengths ranging from 0.1 ms to 0.6 ms. The echo intensity was proportional to fish density below certain density limits. At high fish density a shadowing effect was observed. Factors encountered during survey work on schooling fish which indicate shadowing are also discussed.

The exact density values at which shadowing occurs, appear to depend on parameters such as fish species, size, orientation, and probably also the vertical extention of the school.

INTRODUCTION

The basic principle of acoustic fish stock estimation when using echo integration is that the relation between the integrated echo intensity, M, and the fish density, ϱ, is (Midttun and Nakken 1971)

$$\varrho = C \cdot M$$

where C is the density coefficient. It expresses the number of fish per unit area which contributes to one unit of the integrated echo intensity. It is dependent upon fish species and size and the characteristics of the sounder and integration system (Nakken 1975). In dense schools one may expect, due to acoustic interaction of the individual fish, that the members of the deeper part of the school are shadowed by the members which are nearer the transducer. This may take form of scattering and absorption of sound energy by the nearer members, and consequently the lower fishes will reflect less sound energy per density unit. This will lead to an underestimation of fish density.

Little is known about the effects of acoustic interaction of fish in a school (McCartney, Stubbs and Tucker 1965). Some teoretical work

on scatterers have been done, the scatterers usually being point scatterers or small bubbles, and WESTON (1967) has applied the results for bubbles to fish schools. However, little experimental work has been done in this field (LOVE 1971).

The aim of the present investigation has been, by means of acoustic measurements of live fish, to examine if the proportionality between fish density and integrated echo intensity is valid at all fish densities.

MATERIALS AND METHODS

The materials treated in this investigation is:

1) Echograms and oscilloscope readings obtained during survey on schooling fish with a research vessel.
2) Fully controlled measurements of echo intensity from known densities of fish.

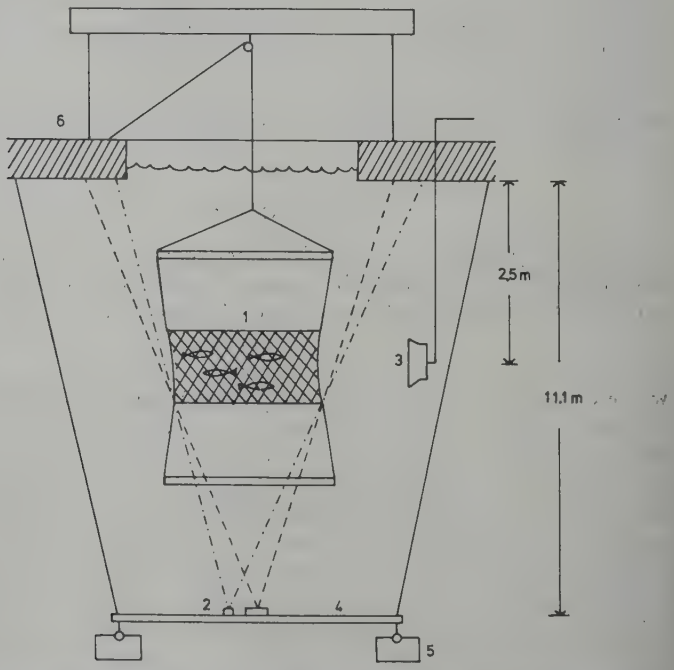

Fig. 1. Experimental arrangement (not to scale). 1) Net cage, 2) transducers, 3) camera, 4) transducer base, 5) load, 6) raft.

Table 1. Data for the net cages.

	Distance between supporting rings (m)	Height of net cage (m)	Diameter of net cage at top and bottom (m)	Diameter of net cage at the centre (m)	Mesh size (mm)	Volume of net cage (m^3)
Net cage 1 (saithe)	3.80	1.80	1.45	1.40	14	2.87
Net cage 2 (sprat)	3.40	2.40	1.50	1.40	26	3.96

Table 2. Mean length (l), standard deviation (SD), mean weight ($\bar{w}$) of fish used during the acoustic measurements.

Species	l (cm)	SD (cm)	$\bar{w}$ (g)
Saithe	35.1	0.6	375
Sprat	12.1	1.7	12

The controlled measurements were carried out from an anchored raft. A diagram (not to scale) of the experimental arrangement is shown in Fig. 1. The upward looking transducers were mounted on a heavily loaded steel frame submerged from the raft in adjustable wires. The net cage was suspended on a line on the acoustic axis of the sound beam at a mean depth of 2.5 m. Table 1 gives data for the two net cages. The upper and lower metal supporting rings were placed at some distance from the net cage; thus the echoes from these rings were not included in the integration interval. Before an acoustic measurement was made, the net cage was hoisted to the surface, and the desired amount of fish was transferred through an opening on the top of the net cage. Then the net cage was lowered to the desired depth.

The acoustic measurements were carried out on two species, saithe (*Pollachius virens*) and sprat (*Sprattus sprattus*). Length and weight data of the fish are shown in Table 2. Before the measurements the fish were kept in floating pens where the fish were acclimatized to the depth at which the measurements were made.

The mean depth of the net cages during the measurements was 2.50 m. At the mean depth the diameter of the net cages was 1.40 m (Table 1), and the sound level at the rim of the cage was measured to be approximately one dB down compared with the sound level at the acoustic axis.

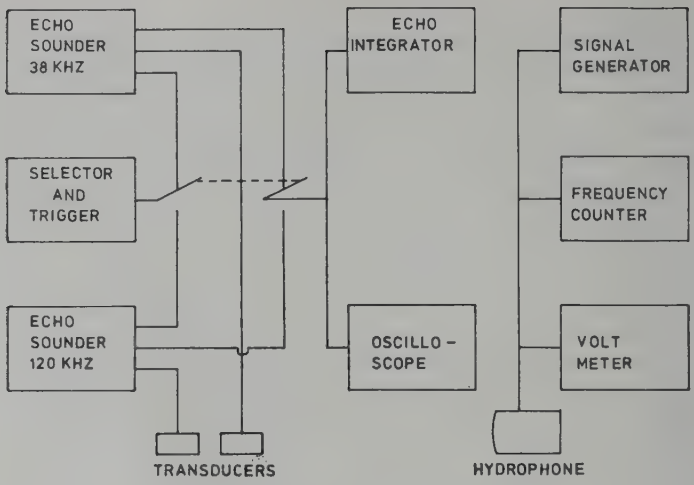

Fig. 2. Block diagram of instrumentation.

A block diagram of the instrumentation is shown in Fig. 2, and Table 3 gives instrument data and control settings.

RESULTS

Fig. 3 shows drawings of four oscilloscope readings of capelin (*Mallotus villosus*) schools. The volt scale is horisontal and the time scale vertical, the vertical extention of the schools being in the order of 30—40 m.

Fig. 4 shows a echogram recording of large schools of spawning capelin on the coast of Finnmark, Northern Norway. The vertical extention of the schools varies from 25 m to 70 m.

Fig. 5—8 show the integrated echo intensities (sum of 1200 pulse transmissions) obtained during the controlled experiments for the different fish densities. In order to compare the different frequencies and pulse lengths, the echo intensities are given in relative values, i.e. the maximum value for each series is set at 1.0. The densities at which the proportionality between integrated echo intensity and fish density is no longer valid, here called shadowing densities, are summarized in Table 4.

For saithe there was only one series of measurements, but for sprat the series was repeated. The values in Fig. 5 and 6 are mean values. The variation of the integrated echo intensities of single pulse transmissions from constant fish densities will be discussed in a later paper.

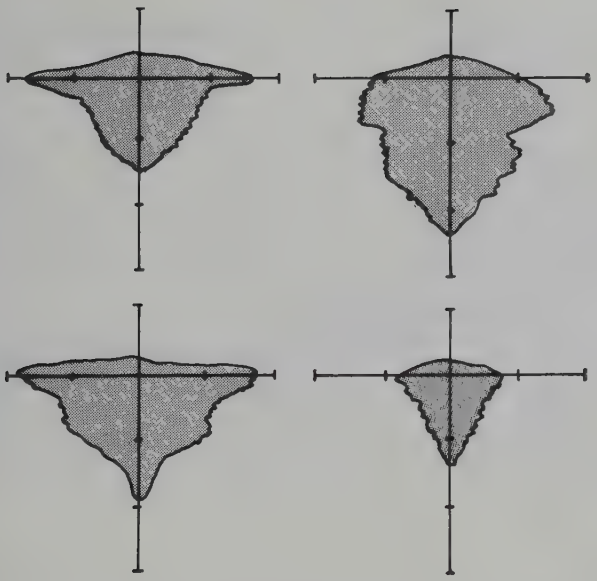

Fig. 3. Oscilloscope readings of capelin schools, Barents Sea, February 1974. 38 kHz 0.6 ms. Volt scale horisontally, time scale vertically.

Table 3. Instrument data and control settings.

Echo sounder:	
Type:	Simrad EK 38A and EK 120A
Frequency:	38 kHz and 120 kHz
Transducers:	10 cm × 10 cm (38 kHz). Circular, diameter 5 cm (120 kHz)
Mode:	WL
Discriminator:	1
Pulse lengths:	0.3 ms and 0.6 ms (38 kHz), 0.1 ms and 0.6 ms (120 kHz)
Bandwidth:	Wide
Output power:	1/10
Repetition rate:	4 pulses per second
Echo integrator:	
Type:	Simrad QM Mk II
Mode:	1 (Channel A. Sounding, Channel B. Nautical mile)
Speed Comp.:	10 knots
Reset:	Manually after 5 minutes (1200 pulses)

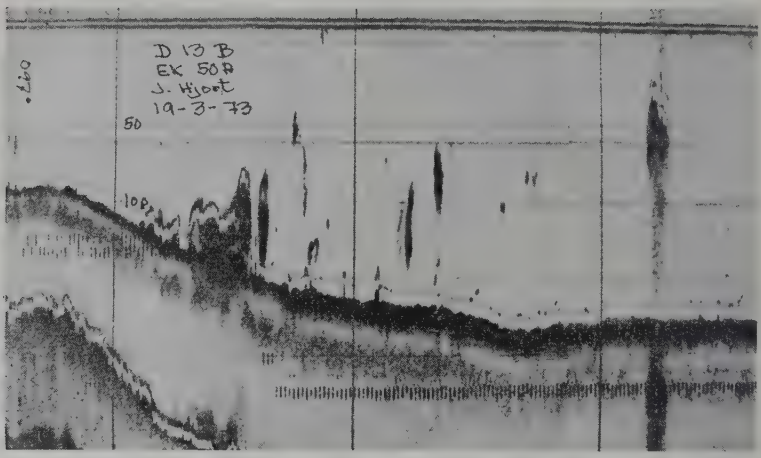

Fig. 4. Echogram of school of spawning capelin, Finnmark coast, March 1973. Depth scale in meters.

Table 4. Shadowing densities for saithe and sprat.

Species	Frequency (kHz)	Pulse length (ms)	Shadowing density	
			Fish/m³	kg/m³
Saithe	38	0.3	110— 130	41—49
	38	0.6	100— 120	38—45
	120	0.1	130— 140	49—53
	120	0.6	120— 130	45—49
Sprat	38	0.3	1800—2100	22—25
	38	0.6	1800—2000	22—24
	120	0.1	2700—2900	32—35
	120	0.6	2400—2600	29—31

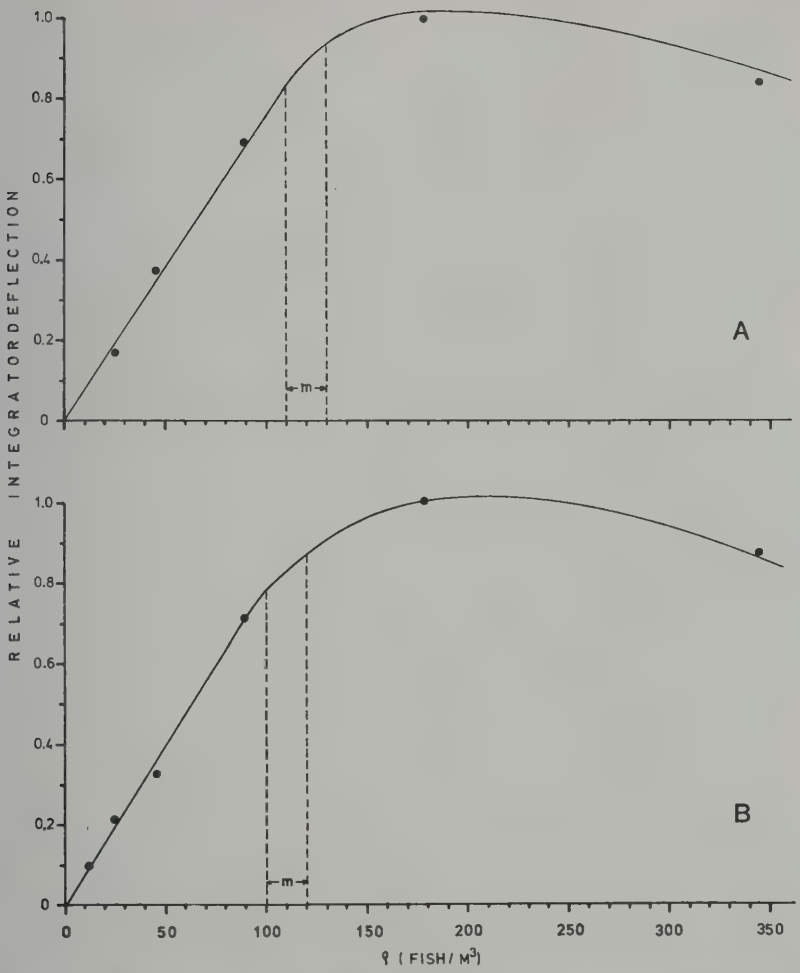

Fig. 5. Observations of relative integrator deflection on densities of saithe at 38 kHz. A) 0.3 ms, B) 0.6 ms, m) density values at which shadowing was encountered.

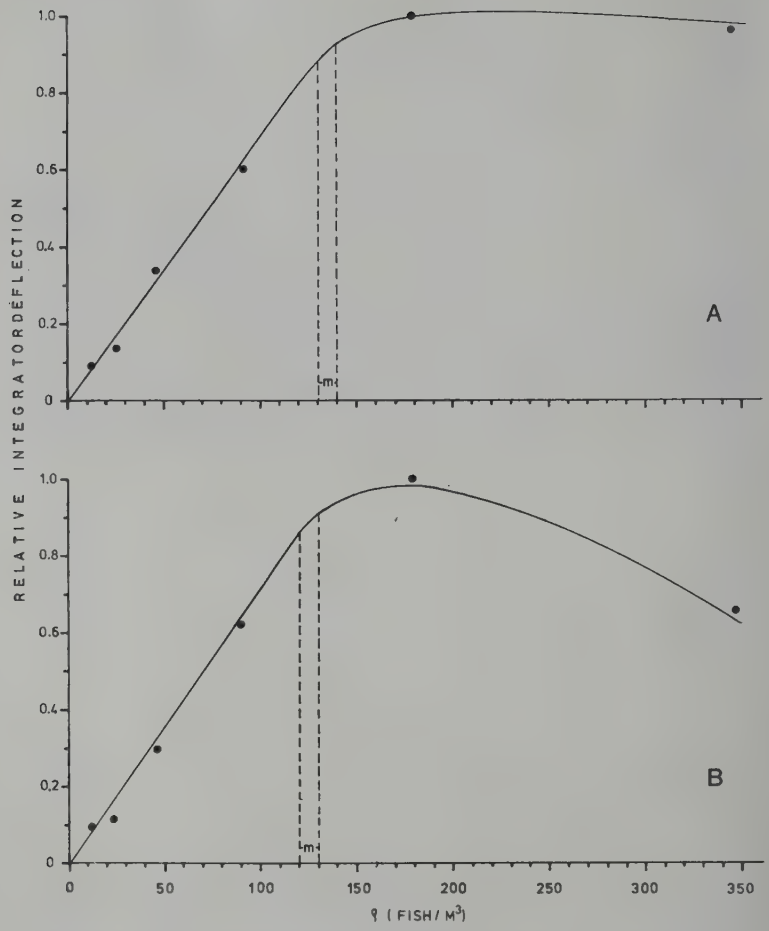

Fig. 6. Observations of relative integrator deflection on densities of saithe at 120 kHz. A) 0.1 ms, B) 0.6 ms, m) density values at which shadowing was encountered.

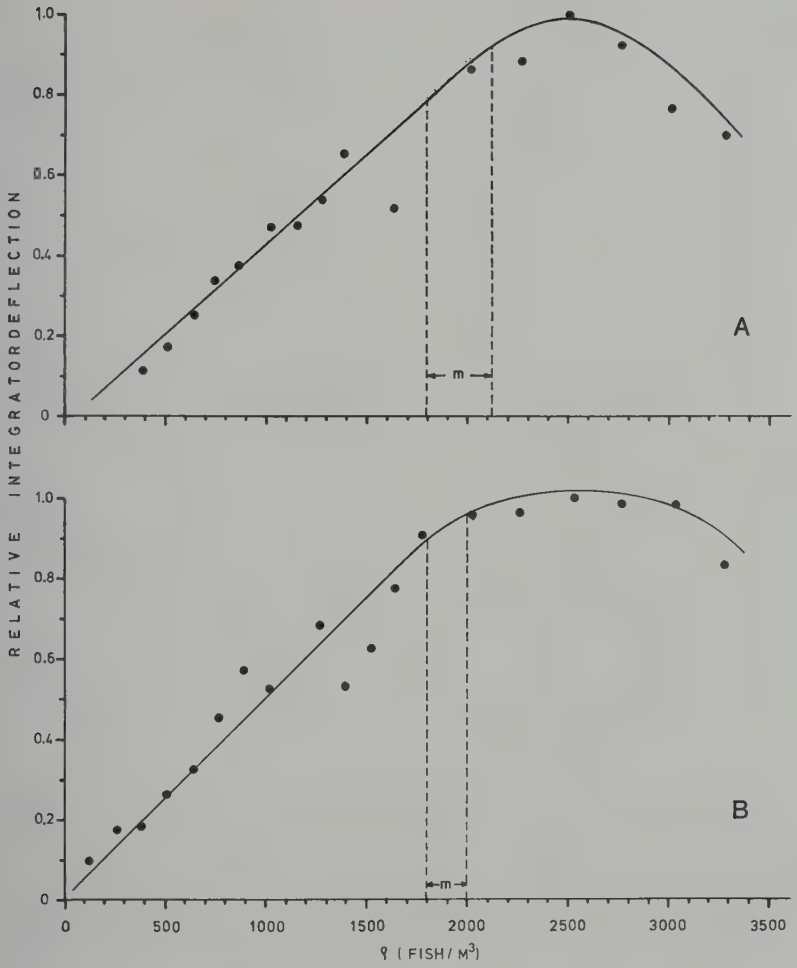

Fig. 7. Observations of relative integrator deflection on densities of sprat at 38 kHz. Legend as in Fig. 5.

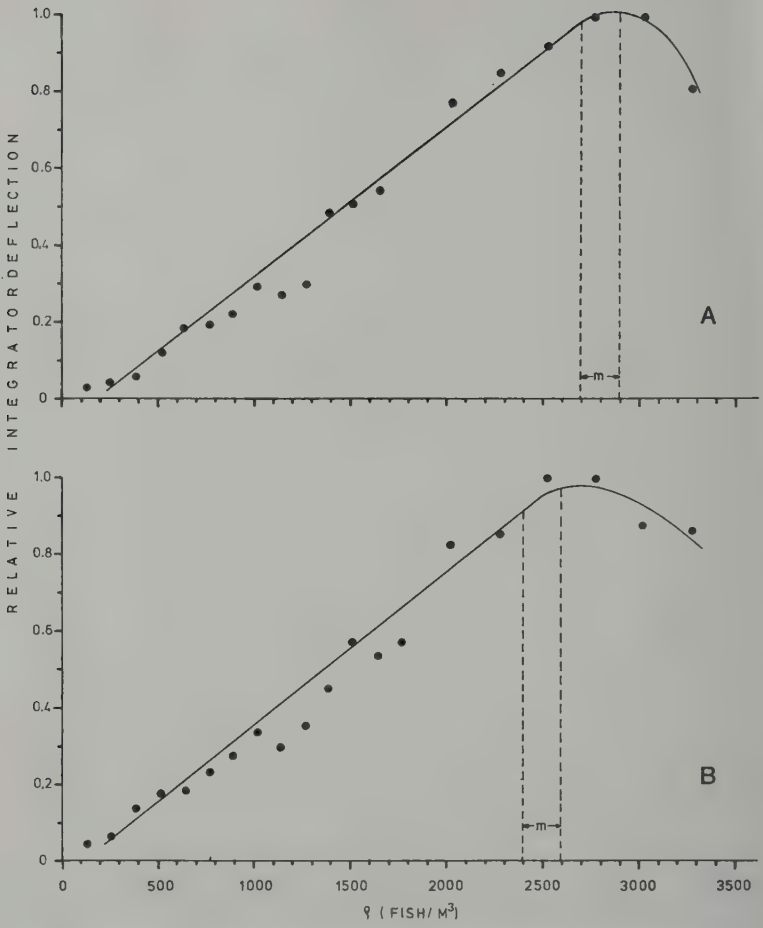

Fig. 8. Observations of relative integrator deflection on densities of sprat at 120 kHz. Legend as in Fig. 6.

DISCUSSION

There are strong reasons to believe that shadowing effects are encountered during surveys on fish schools. The schools in Fig. 3 all show less sound reflection from the deeper layers. The echo sounder has an automatic depth compensator, and it is doubtful if the oscilloscope readings show the actual physical structure of the school, i.e. with greater fish density in the upper layers of the school. A more plausible explanation would be that sound energy is attenuated within the school.

The modern echo sounder is equipped with a white line function. The purpose of this function is to make it easier to discriminate fish which are close to the bottom, and, of great importance when making fish stock assessments with integrator techniques, to prevent strong bottom signals from being integrated. The bottom has a clear white line in areas with no capelin in Fig. 4. However, below the capelin school this bottom white line disappears. This means that the strength of the bottom echo is considerably reduced, and it is therefore probable that the echo of lower fishes will also be reduced. This is the shadowing effect which was discussed in the introduction of this paper. The figure shows also that the echo from the upper part of the schools is so strong that it is blocked.

By using integrator technique the density in the capelin school will be considerably underestimated due to

A. Blocking of the uppermost layer;
B. Shadowing of the lower fishes by the members of the school which are nearer the transducer.

A can be avoided by an appropriate altering of the discriminator level, while the quantitative effects of B are much more difficult to estimate.

The large school in Fig. 4 is a spawning school of capelin. The structure of these spawning schools has been well studied by direct observation by SCUBA divers (BAKKE and BJØRKE 1973, SÆTRE and GJØSÆTER 1975). The densities of these schools are tabulated in Table 5 together with other direct or indirect observations of fish density.

As discussed earlier there is a reduction of the bottom signal below the large capelin school in Fig. 4. This type of spawning school is what SÆTRE and GJØSÆTER (1975) call a "first type school", and these schools consisted of more or less regularly oriented capelin swimming forward or in circles. BAKKE and BJØRKE (1973) and SÆTRE and GJØSÆTER (1975) give densities in distances between fishes. A distance of 15 cm (Table 5) between capelin of 15 cm length will give a density of about 150—200 fish/m^3. This is considerably lower than the shadowing densities given for sprat in Table 4. The sprat is only a little smaller than capelin, and this

Table 5. Natural fish densities.

Species	fish/m³	kg/m³	Interfish distance (cm)	References
Mallotus villosus			40—80 Spawning schools (first type)	Bakke and Bjørke (1970)
M. villosus			10 Spawning schools (second type)	Bakke and Bjørke (1970)
M. villosus			15—30 Spawning schools (first type)	Sætre and Gjøsæter (1975)
M. villosus			5 Spawning schools (second type)	Sætre and Gjøsæter (1975)
Clupea harengus	0.7—1.0			Truskanov and Scherbino (1966)
C. pallasi		0.2—0.8		Radakov (1973)
C. pallasi		30—32 (2—3 days before spawning)		Radakov (1973)
C. pallasi	9.0—10.4 (day)			Thorne (1973)
C. pallasi	0.012—1.0 (night)			Thorne (1973)
Engraulis encrasicholus	650			Johannesson and Losse (1973)
E. mordax	50—75			Mais (1973)
Sardina pilchardus	2		80	Cushing (1957)
Merluccius productus		0.04—0.05		Thorne (1973)
Gadus morhua	$1.0—8.0 \cdot 10^{-5}$			Truskanov and Scherbino (1966)
Trachurus mediteranus	110			Johannesson and Losse (1973)
Scomber japonicus	20			van Olst and Hunter (1970)

seems to suggest that the shadowing effect is not due to density as such, but rather to the total number of fish or scatterers within the sound beam. In schools with a great vertical extention, such as the spawning school in Fig. 8, shadowing effects may then well be encountered at lower densities than in schools with a short vertical extention like those observed during the experiment.

The problem of estimating densities at which shadowing occurs at different school extentions may be approached by an application of the mathematical theory of multiple scattering. By using the same number of fish which gave a shadowing effect during the experiments, one could make a density reduction by analysing reflection from the same number of scatterers at different fictive extentions of the net cage.

To apply such results to field work, one would probably need exact information of species, sizes of the schools, length distribution, absorption patterns of the fish etc. In addition, behavioral information would be needed, such as orientation and mobility of the fish. At present, much of this information is lacking.

The curves obtained by using different pulse lengths and frequencies do not seem to have significant differences within the same species. There may be a tendency that the shadowing effect first occurs at higher densities when using higher frequencies (Table 4). The curves show decreasing echo intensity for the highest densities. The exact reason for this is unknown.

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STOCK SIZE FLUCTUATIONS AND RATE OF EXPLOITATION OF THE NORWEGIAN SPRING SPAWNING HERRING, 1950—1974

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ABSTRACT

DRAGESUND, O. and ULLTANG, Ø. 1978. Stock size fluctuations and rate of exploitation of the Norwegian spring spawning herring, 1950—1974. *FiskDir. Skr. Ser. HavUnders.*, *16*: 315—337.

The collapse of the Norwegian spring spawning herring stock is described, followed by a discussion of the causes. Stock size and fishing mortality were calculated from virtual population analysis for the years 1950—1974. The analysis showed that the young herring fishery had a serious effect on the recruitment to the adult stock during the whole period. The 1961 year class was the last one which survived the small- and fat-herring fisheries in any quantity.

The fishing mortalities on the adult stock were at a low or moderate level until 1964. Thereafter a rapid increase in the fishing mortalities took place, primarily as a result of the escalation in the summer and autumn fisheries off Iceland.

The result of the investigation leaves no doubt that the fishing pressure was the primary factor for the collapse of this herring stock.

INTRODUCTION

Traditionally the main fishery on the adult stock of Norwegian spring spawning herring took place in winter along the Norwegian west coast prior to and during the spawning season (DEVOLD 1963). Another important fishery, the summer and autumn herring fishery, took place on the feeding grounds along the Polar front in the Norwegian Sea. This fishery was for a long period located off northern and northeastern Iceland exploiting mainly the adult stock (JAKOBSSON 1963). During the last two decades there has been a drastic change in the migration pattern of the adult stock, and this has strongly influenced the location of the summer and autumn as well as the winter herring fishery (DEVOLD 1968, JAKOBSSON 1968).

Although the total catch of adult herring (including the summer and

Table 1. Total catch in thousand metric tons of adult Norwegian spring spawning herring 1950—1971.

Year	Iceland	Norway	USSR	Faroes	Fed. Rep. of Germany	Total
1950	30.7	781.4	14.0	—	—	826.1
1951	48.9	902.3	43.0	—	—	994.2
1952	9.2	840.1	69.9	—	—	919.2
1953	31.5	692.2	110.0	16.2	—	849.9
1954	15.2	1 103.6	160.0	27.6	—	1 306.4
1955	18.1	979.3	207.0	13.1	—	1 217.5
1956	41.2	1 160.7	235.0	23.7	—	1 460.6
1957	18.2	813.1	300.0	17.0	—	1 148.3
1958	22.6	356,7	388.0	17.7	—	785.0
1959	34.5	426.9	408.0	13.7	—	883.1
1960	26.7	318.4	465.0	11.0	—	821.1
1961	85.0	111.0	285.0	16.9	—	497.9
1962	176.2	156.2	209.0	9.8	—	551.2
1963	177.5	130.4	350.0	12.9	—	670.8
1964	367.4	366.4	365.8	18.3	—	1 117.9
1965	540.0	259.5	489.2	31.5	5.6	1 325.8
1966	691.4	497.9	447.4	60.7	26.1	1 723.5
1967	359.3	423.7	303.9	34.9	9.7	1 131.5
1968	75.2	55.7	124.3	16.1	1.8	273.1
1969	0.6	15.6	3.2	4.4	0.3	24.1
1970	—	20.3	—	0.6	—	20.9
1971	—	6.9	—	—	—	6.9

autumn fishery) has to a large extent fluctuated in relation to the entrance of strong year classes throughout the history of the fishery (ØSTVEDT 1963), this phenomenon has been especially pronounced during the period 1950—1970 (ANON. 1970). Thus the very rich 1950 year class caused high catches in the adult herring fisheries in the mid 1950s, and the strong year classes of 1959 and 1960 gave high yields in the years 1964—1967 (Table 1). Both periods of high catches were followed by a decline which was most striking in the latter period when the decrease in the adult stock was accelerated by an increase in exploitation rate compared to earlier periods. However, the decline was primarily caused by practically no recruitment to the adult stock after the 1959 and 1960 year classes were fully recruited to the stock in 1966.

From 1965 onwards a rapid decrease in the stock size took place, and in 1969—1971 the catches in both the adult summer and winter herring fisheries were negligible compared with those of earlier years. During the spawning season of 1972 almost no herring were recorded on the traditional spawning grounds, and the spawning stock was reduced to an extraordinari-

Table 2. Catches in thousand metric tons of small and fat herring taken by Norway and USSR 1950—1974. Herring caught south of Stad are excluded except for Norwegian small herring catches in 1950—1959.

Year	Small herring			Fat herring			Grand total
	Norway	USSR	Total	Norway	USSR	Total	
1950	72.9	—	72.9	29.7	4.3–	34.0	106.9
1951	190.1	10.5	200.6	80.5	2.5	83.0	284.2
1952	276.4	2.1	278.5	55.2	1.9	57.1	335.6
1953	147.0	3.8	150.8	84.7	5.2	89.9	240.7
1954	190.1	8.8	198.9	138.0	1.2	139.2	338.1
1955	94.3	3.0	97.3	36.0	9.0	45.0	142.3
1956	86.8	—	86.8	102.0	10.0	112.0	198.8
1957	118.5	3.8	123.3	46.4	1.5	47.9	171.2
1958	133.5	8.1	141.6	55.1	4.6	60.0	201.6
1959	164.5	7.2	171.7	46.8	9.5	56.3	228.0
1960	212.0	5.7	217.7	62.2	0.8	63.0	280.7
1961	222.7	0.9	223.6	108.5	0.1	108.6	332.2
1962	124.5	0.7	125.2	171.3	0.9	172.2	297.4
1963	157.9	—	157.9	143.8	12.0	155.8	313.7
1964	106.8	—	106.8	56.9	0.2	57.1	163.9
1965	116.9	—	116.9	94.3	10.7	105.0	221.9
1966	61.7	—	61.7	147.9	21.9	169.8	231.5
1967	107.1	—	107.1	346.0	92.6	438.6	545.7
1968	26.3	—	26.3	341.1	71.7	412.8	439.1
1969	14.4	—	14.4	21.2	8.1	29.3	43.7
1970	5.2	—	5.2	36.2	—	36.2	41.4
1971	1.1	—	1.1	13.1	—	13.1	14.2
1972	3.3	—	3.3	9.9	—	9.9	13.2
1973	0.3	—	0.3	6.6	—	6.6	6.9
1974	0.6	—	0.6	5.7	—	5.7	6.3

+ Average catch for the period 1941—1950.

ly low level. In 1973—1975 a slight increase in the spawning stock took place due to recruitment from the 1969 year class. (Anon. 1974, 1975 a, 1976.)

In addition to the fishery on adults there was a fishery on young and adolescent herring in the Norwegian fjords, mainly in northern Norway. This fishery is based on the small-herring (småsild), i. e. mainly 0- and I-group fish, and on the fat-herring (feitsild), i. e. I- to IV-group herring (Dragesund 1970). The catches of small-herring have declined since the mid 1960s (Table 2). This decline was largely determined by the low abundance of small-herring due to a series of weak to moderate year classes after 1965. Catches of the fat-herring increased considerably in the years 1966–1968 after having fluctuated with no definite trend in the years 1950—1965 (Table 2).

The description of the collapse of the stock of Norwegian spring spawning herring is well documented in several reports (ANON. 1970, 1972, 1975 b). The aim of the present paper is to give an analysis of the effect of the fishery on the stock during the period 1950—1974.

MATERIALS AND METHODS

Stock size and fishing mortality were calculated from Virtual Population Analysis (VPA), the main input data being the total catch in number by age in the different years. Catches in weight were converted separately to catch in number by age for the adult fisheries and the young and adolescent herring fisheries (small- and fat-herring).

The catch in number by year class in the adult fisheries from 1962 to 1970, given by the Working Group on Atlanto-Scandian Herring (ANON. 1970, 1972), was extended to cover the period 1950—1971 and all age groups in the adult fisheries (Table 3) by utilizing:

(i) Data on age composition in the winter fishery 1950—1970 and the summer and autumn fishery 1962—1970 given in ANON. (1970, 1972).
(ii) Data on mean weight of herring from the winter fishery 1950—1961 available from the records of Institute of Marine Research, Bergen.
(iii) Icelandic data on age composition in the summer and autumn fishery in 1950—1961 as reported in Annales Biologiques (ANON. 1951—1954, ANON. 1956—1963).
(iv) Icelandic data on mean weight by age during the summer and autumn fishery (JACOBSSON, personal communication).
(v) Data on age composition and mean weight in catches from the Norwegian winter fishery 1971.

The catch in number by year class in the young and adolescent herring fisheries in 1950—1974 (Table 4) were obtained by utilizing:

(i) Data on catch by year class in the small-herring fishery given in DRAGESUND (1970) and data from the records of the Institute of Marine Research, Bergen.
(ii) Data on age composition in the fat-herring fishery given in DRAGESUND (1970) and data from the records of the Institute of Marine Research, Bergen.
(iii) Data on mean weight by month and district for year classes going through the small- and fat-herring fisheries from the 0-group to the adolescent stage given in DRAGESUND (1970).

A constant natural mortality of $M=0.16$, as estimated by the Working Group on Atlanto-Scandian herring (ANON. 1970), was assumed for the whole period 1950—1974 for all age groups. The Working Group arrived at the estimate by utilizing data on catch in number by age for 4 years old and older herring. It is, therefore, uncertain how representative the figure 0.16 is for younger age groups.

Table 3. Catch in numbers (millions) of Norwegian spring spawning herring in the adult fisheries 1950—1971.

Year class	Year							
	1950	1951	1952	1953	1954	1955	1956	1957
1930	3.6							
1931	0.9	0.5						
1932	18.5	8.7	3.8					
1933	42.4	18.4	28.1	22.2				
1934	171.9	158.0	127.7	95.4	63.2			
1935	107.0	119.5	83.2	89.6	80.0	43.0		
1936	66.4	47.4	65.3	73.8	89.2	72.6	45.0	
1937	368.3	348.0	256.3	233.9	247.4	104.6	75.7	31.3
1938	194.5	253.5	186.5	215.5	196.6	141.6	137.5	52.0
1939	86.9	107.6	106.8	98.8	126.8	115.2	122.8	61.8
1940	109.5	103.1	107.7	94.1	133.0	103.6	95.2	60.1
1941	88.6	82.7	85.7	91.2	100.6	84.6	88.9	42.5
1942	79.5	77.1	79.2	61.7	88.4	58.7	63.0	33.7
1943	628.6	602.0	377.9	394.9	460.7	203.2	163.3	131.6
1944	547.0	515.6	380.2	314.1	440.4	295.6	272.8	149.3
1945	185.5	164.4	204.5	110.9	199.8	193.4	198.3	121.2
1946	184.8	172.4	136.3	81.9	128.1	85.5	130.7	88.4
1947	276.2	383.8	602.3	355.6	490.3	274.7	264.2	182.5
1948		6.6	60.5	100.9	236.0	189.6	203.9	127.3
1949			39.3	46.6	142.9	114.3	110.0	72.0
1950				98.2	1 083.9	1 954.3	2 375.4	1 946.4
1951					55.8	262.2	275.8	220.5
1952						62.4	232.7	144.0
1953							27.9	246.1
1954								13.0
1955								
1956								
1957								
1958								
1959								
1960								
1961								
1962								
1963								
1964								
1965								
1966								
1967								
1968								
Total	3 160.1	3 169.3	2 931.1	2 579.3	4 363.1	4 358.8	4 883.1	3 723.7

Table 3 (cont.)

Year class	year						
	1958	1959	1960	1961	1962	1963	1964
1930							
1931							
1932							
1933							
1934							
1935							
1936							
1937							
1938	32.7						
1939	27.7	27.6					
1940	46.6	27.7	15.1				
1941	44.9	31.2	19.9	2.1			
1942	34.3	22.6	19.8	3.4	5.1		
1943	69.4	41.6	27.9	4.5	13.5	1.9	
1944	70.9	85.2	39.0	12.7	16.8	7.7	10.8
1945	77.4	77.4	47.2	15.7	30.3	19.3	14.3
1946	98.7	88.5	56.7	21.7	30.3	25.1	7.2
1947	200.9	198.0	153.5	63.0	79.2	61.8	46.6
1948	123.0	124.3	129.7	45.0	64.1	60.6	43.2
1949	70.7	88.6	85.2	49.7	49.3	79.8	46.1
1950	959.1	1 084.8	1 163.0	727.6	959.3	932.7	771.6
1951	192.9	239.7	203.9	136.1	138.9	174.1	151.9
1952	87.5	113.8	73.2	49.2	59.8	92.5	83.2
1953	100.3	138.0	93.8	61.5	64.1	107.7	96.3
1954	16.1	24.6	21.6	19.4	13.3	9.3	29.3
1955	8.0	22.8	23.3	14.9	20.2	18.3	24.9
1956		7.0	4.0	4.1	6.5	3.5	3.0
1957				1.8	2.0	1.7	1.5
1958					1.4	4.9	13.1
1959					255.7	408.9	1 917.7
1960					49.8	38.2	307.6
1961							90.2
1962							2.2
1963							
1964							
1965							
1966							
1967							
1968							
Total	2 261.1	2 443.4	2 176.8	1 232.4	1 859.6	2 048.0	3 660.7

Table 3 (cont.)

Year class	Year						
	1965	1966	1967	1968	1969	1970	1971
1930							
1931							
1932							
1933							
1934							
1935							
1936							
1937							
1938							
1939							
1940							
1941							
1942							
1943							
1944							
1945	4.3						
1946	8.7	5.5					
1947	21.7	16.5					
1948	52.1	8.8					
1949	70.2	14.9	1.9				
1950	703.0	392.7	64.3	5.4	1.1	0.2	
1951	137.7	96.9	14.3	4.1	0.2	—	
1952	106.9	72.1	14.3	3.6	0.3	0.1	0.02
1953	100.5	69.1	17.5	1.8	0.2	0.1	0.02
1954	40.0	11.0	8.9	2.6	—	0.1	0.02
1955	19.1	26.1	8.5	2.5	0.3	0.1	0.06
1956	7.4	17.4	3.5	0.8	0.2	0.1	—
1957	14.9	14.4	5.7	1.1	0.3	0.1	0.02
1958	19.5	38.0	8.9	2.0	—	0.1	—
1959	2 195.8	2 868.3	1 718.2	345.9	36.3	28.2	5.45
1960	570.4	1 290.6	1 135.0	134.8	33.5	26.7	6.91
1961	245.9	459.1	422.2	93.9	11.6	13.2	4.41
1962	12.1	26.1	27.0	14.3	0.7	1.0	0.36
1963	45.1	80.6	25.7	15.2	2.9	3.3	1.13
1964					—	0.4	1.01
1965					0.2	0.3	0.36
1966						1.3	0.94
1967						0.2	0.62
1968							0.32
Total	4 375.3	5 508.1	3 475.9	628.0	87.8	75.5	21.65

Table 4. Catch in numbers (millions) of Norwegian spawning spring herring in the young herring fisheries (small- and fat- herring) 1950–1974.

Year class	Year												
	1950	1951	1952	1953	1954	1955	1956	1957	1958	1959	1960	1961	1962
1950	5 112.6	7 607.7	1 232.9	641.9	351.6	90.8	179.7	38.9	14.4	19.0	—	0.5	
1951		1 635.5	9 149.7	581.3	210.5	14.2	38.4	8.0	1.5	1.0	—	—	
1952			13 721.6	5 055.0	855.4	30.6	18.9	9.8	1.8	1.0	0.1	—	
1953				5 697.2	7 071.1	510.1	88.6	127.2	10.6	8.6	2.4	0.1	
1954					10 676.0	2 871.1	627.1	10.3	1.8	1.3	2.8	—	
1955						5 175.6	2 023.7	219.5	9.5	4.0	4.8	0.1	
1956							5 363.9	3 290.8	666.4	8.1	14.2	—	
1957								5 001.9	2 798.1	325.5	121.7	6.3	0.7
1958									9 667.0	1 985.3	392.5	31.2	6.6
1959										17 896.3	13 580.8	2 884.8	1 641.1
1960											12 884.3	16 075.6	1 006.5
1961												6 207.5	4 049.2
1962													3 687.5
Total	5 112.6	9 243.2	24 104.1	11 975.5	19 164.6	8 692.5	8 340.2	8 706.4	13 171.1	20 250.1	27 003.5	25 206.1	10 391.6

Year class	Year											
	1963	1964	1965	1966	1967	1968	1969	1970	1971	1972	1973	1974
1956	0.1											
1957	0.1											
1958	0.4	0.6										
1959	422.8	128.1	4.1	9.6								
1960	722.2	91.4	0.7	17.2								
1961	2 051.7	24.4	10.3	5.9								
1962	2 122.3	218.1	78.0	1.1								
1963	4 811.0	2 728.3	2 806.5	1 957.8	3 241,4	1 367,2	1,8					
1964		3 613.	3 752.0	1 671.0	1 395.5	1 900.6	8.9	2.9	0.1	0.5		
1965			2 303.0	664.0	70.3	98.8	0.6	0.3	—	0.2		
1966				3 893.0	9 911.1	385.4	188.1	17.3	0.3	1.0	0.1	
1967					428.0	435.3	142.2	6.4	0.4	2.2	0.4	
1968						1 782.0	507.9	33.5	1.5	1.6	0.1	
1969							555.9	530.1	85.1	33.6	10.9	5.3
1970								118.9	42.9	8.5	0.8	0.2
1971									30.5	52.3	0.3	0.1
1972										178.5	25.3	10.4
1973											18.0	23.1
1974												37.8
Total	10 130.5	6 803.9	8 954.5	8 219.0	15 046.3	5 969.2	1 405.3	709.4	160.8	278.4	56.0	77.0

Table 5. Spawning stock size in number ($N \times 10^{-9}$) and weight (million metric tons) and fishing mortality 1950—1971. The figures in brackets are uncertain because of the information for the VPA being from only a few years catches.

Year	Spawning stock size		Fishing mortality			
	Number	Weight	4 years old	5 years old	6 years old	7 years old and older
1950	36.9	9.4	0.054	0.047	0.091	0.095
1951	30.3	9.1	0.050	0.062	0.051	0.12
1952	28.8	8.8	0.014	0.098	0.061	0.12
1953	23.5	7.1	0.016	0.028	0.074	0.14
1954	27.0	7.6	0.038	0.059	0.082	0.22
1955	34.1	8.8	0.051	0.067	0.058	0.17
1956	32.3	8.9	0.10	0.072	0.11	0.21
1957	35.8	10.0	0.17	0.079	0.066	0.13
1958	28.7	8.5	0.040	0.065	0.057	0.097
1959	23.3	7.5	0.074	0.072	0.110	0.13
1960	17.3	5.6	0.16	0.10	0.087	0.15
1961	13.1	4.2	0.089	0.048	0.068	0.11
1962	9.9	3.3	0.050	0.037	0.096	0.19
1963	7.5	1.6	0.057	0.041	0.030	0.29
1964	13.6	3.7	0.081	0.18	0.14	0.40
1965	17.8	4.5	0.17	0.15	0.29	0.75
1966	11.2	2.7	0.39	0.51	0.58	0.83
1967	4.8	1.3	1.1	0.80	1.2	1.5
1968	1.0	0.24	4.5	4.4	1.4	1.1
1969	(0.29)	(0.08)	(0.28)	(0.71)	(0.39)	(0.42)
1970	(0.17)	(0.06)	(1.31)	(0.34)	(0.60)	(0.63)
1971	(0.09)	(0.03)	(0.10)	(0.24)	(0.33)	0.3+

+ Assumed value.

RESULTS

ADULT STOCK

Table 5 shows the spawning stock size in number and weight and the fishing mortality on 4, 5, 6, 7 years old and older herring for the years 1950—1971, assuming a fishing mortality of 0.3 on the fully recruited year classes in 1971. A fishing mortality of 0.3 gives a spawning stock size of about 30 000 tonnes in 1971. The results of the calculations given in Table 5 are also plotted in Fig. 1 (stock size in number), Fig. 2 (stock size in weight) and Fig. 3 (fishing mortality on 7 years old and older herring).

The fishing mortalities are those generated by the total catch of an age group and not only the catch in the adult fisheries. It appears from Table 4 that some 4, 5 and 6 years old herring are also taken in the fat-herring

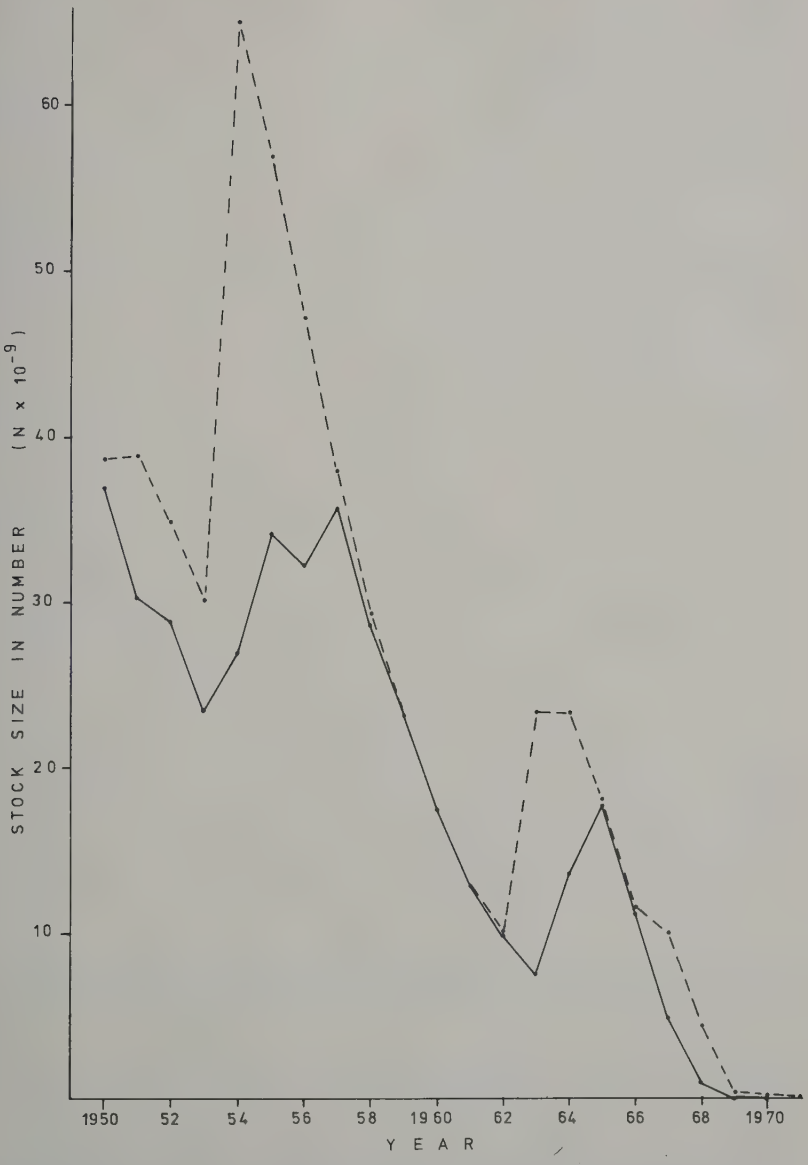

Fig. 1. Spawning stock size in number and total number of 4 years old and older herring (broken line) for the years 1950—1971.

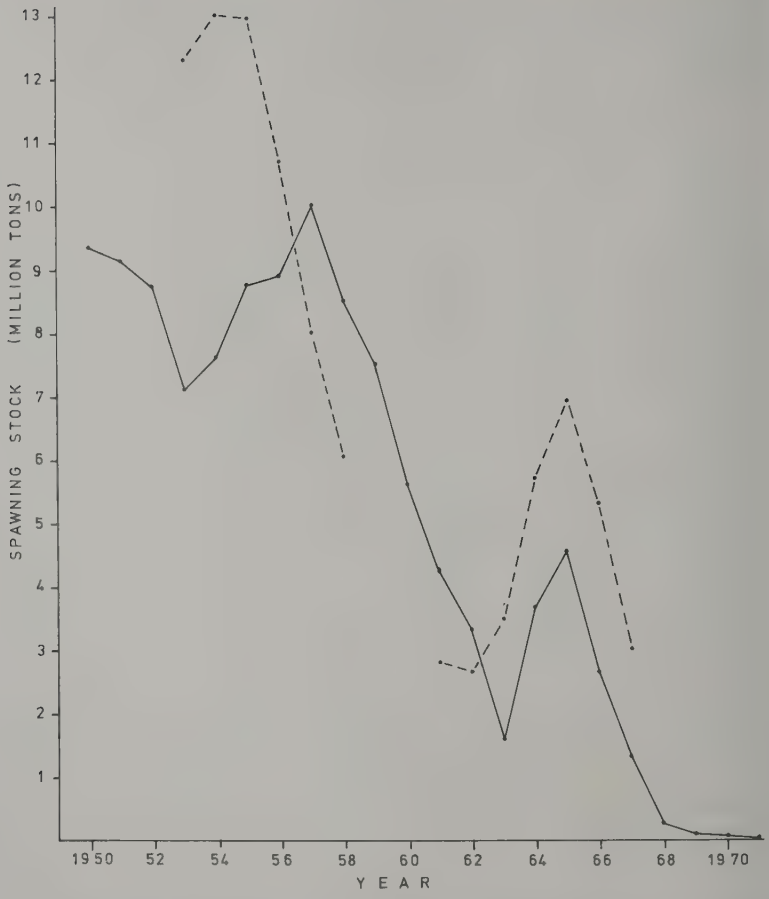

Fig. 2. Spawning stock size in weight for the years 1950—1971. The broken line shows stock size estimates given by the Working Group on Atlanto-Scandian Herring (ANON. 1970, 1972).

fishery. The fishing mortalities on 4–6 years old herring have generally been lower than on 7 years old and older herring. The main reason for this is probably that these age groups show a more oceanic distribution throughout the year than do the older age groups. Thus, they have not been heavily exploited in the fat-herring fishery and have not been fully recruited to the adult stock. The extremely high fishing mortalities on 4 and 5 years old herring in 1968 (Table 5) were generated by the fat-herring fishery.

The spawning stock size was calculated by assuming full recruitment to

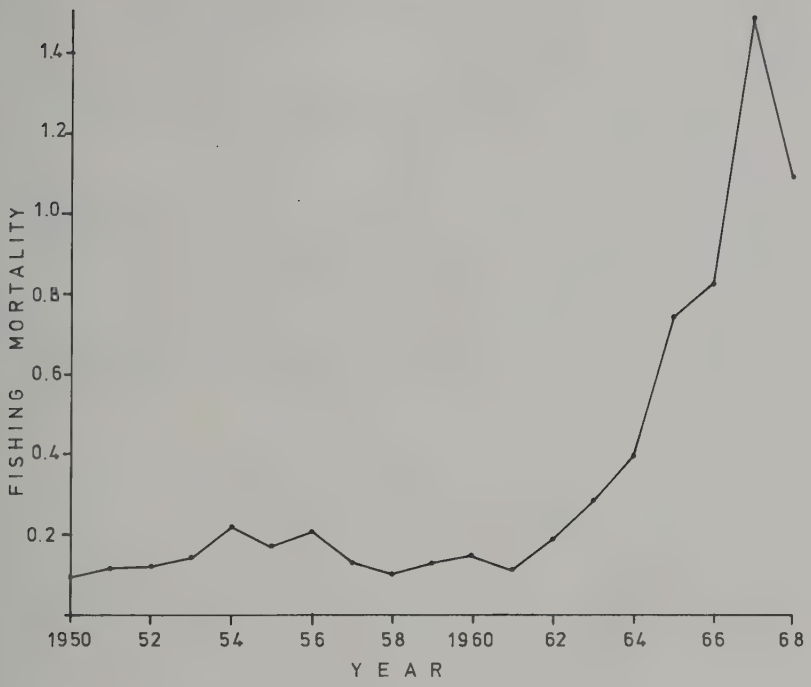

Fig. 3. Fishing mortality on 7 years old and older herring 1950—1968.

the adult stock at an age of 7 years. Portions of the younger year classes were added to the stock size of 7 years old and older herring given by the VPA. The quantity to be added for a year class of age t ($t < 7$) was calculated by:

$$N_t \text{ adult} = \frac{p_t}{p_{7+}} \cdot N_{7+}$$

where N_{7+} = total number of 7 years old and older herring.
p_t = percentage t years old herring in the winter fishery (Table 6).
p_{7+} = percentage 7 years old and older herring in the winter fishery.

The spawning stock size was at a level of about 9 million tonnes in 1950 (Table 5, Fig. 2) and decreased to about 7 million tonnes in 1953. From 1954 to 1957 the strong 1950 year class gradually recruited the spawning stock (Table 6), resulting in an increase in stock size which reached a peak of about 10 million tonnes in 1957 when the year class was fully recruited. The stock then decreased again as a result of poor recruitment, reaching a

minimum level of about 1.6 million tonnes in 1963. The fishing mortalities of the whole period 1950—1963 were on a low or moderate level (Table 5, Fig. 3).

The strong 1959 year class started to recruit to the spawning stock only to a small extent in 1963, but in 1964 it contributed about 60% to the spawning stock in number (Table 6).

The stock increased to about 3.7 million tonnes in 1964 and 4.5 million tonnes in 1965 (Fig. 2) when also the relatively strong 1960 year class recruited to the stock. From 1965 onwards there was a rapid decrease in spawning stock size due to an almost complete stop in recruitment to the adult stock and strongly increasing fishing mortalities. The last year class which recruited to the stock to any extent was that of 1961. The increase in fishing mortalities on the adult stock from 1964 onwards was primarily a

Table 6. Percentage age composition of Norwegian spring spawning herring during the Norwegian winter fishery 1950—1970.

Year Age	1950	1951	1952	1953	1954	1955	1956	1957	1958	1959	1960	1961	1962
2	0.1	—	0.1	0.1	0.1	—	—	0.2	—	—	—	—	—
3	8.3	0.2	1.3	4.0	1.3	1.5	0.6	0.4	0.5	0.4	—	—	0.1
4	5.5	11.6	2.0	1.9	25.2	6.3	5.0	7.4	1.0	1.3	0.3	0.4	—
5	5.5	5.2	19.9	4.1	3.3	46.9	5.9	4.3	6.1	1.4	1.6	0.9	0.5
6	16.3	4.8	4.5	14.4	5.4	2.7	50.6	5.6	4.7	7.5	1.2	3.3	0.9
7	18.7	15.2	6.7	3.2	11.0	4.3	2.3	56.5	6.6	5.1	6.5	2.9	2.5
8	2.3	17.7	12.4	4.2	2.8	5.8	3.9	1.8	50.5	7.8	3.5	7.7	1.5
9	2.5	2.0	12.2	12.0	4.2	1.7	4.6	2.6	2.6	47.3	5.0	4.8	8.0
10	3.1	2.2	2.4	14.4	9.2	4.0	2.2	2.4	3.5	2.2	58.1	6.5	4.0
11	2.4	2.6	2.5	2.0	9.5	5.5	3.5	1.6	3.4	3.3	1.6	59.0	6.6
12	5.4	2.7	3.1	2.8	1.7	3.3	4.1	2.2	2.3	4.5	3.8	4.4	63.5
13	10.4	6.7	3.0	2.9	1.9	1.0	1.9	2.7	2.2	1.9	4.1	3.0	2.1
14	1.6	9.1	5.0	3.0	2.5	1.4	0.9	1.5	1.8	2.3	1.5	2.3	3.6
15	2.7	1.5	7.0	6.6	2.2	1.8	1.2	0.5	1.1	2.2	1.0	1.5	3.4
16	4.8	3.0	1.6	7.0	3.4	1.9	1.4	0.6	0.6	0.9	1.3	1.4	0.7
17	1.1	4.0	2.2	2.2	4.3	2.2	1.7	0.8	0.7	0.5	0.9	0.9	1.0
18	0.5	0.4	3.4	2.9	1.7	1.3	1.6	1.0	0.7	0.7	0.5	0.3	1.0
19	—	0.2	0.8	2.9	1.4	1.5	0.6	0.7	0.5	0.4	0.3	0.4	0.3
20	0.1	—	0.1	0.7	1.0	0.7	0.6	0.3	0.3	0.3	0.5	0.1	—
21	—	0.1	—	0.1	0.1	0.2	0.3	0.2	0.2	0.2	0.3	0.1	0.2
22	—	—	—	—	0.1	0.1	0.1	—	—	0.1	0.1	0.1	—
23	—	—	—	—	—	—	—	—	—	0.1	0.1	—	0.1
?	8.6	10.8	9.8	8.6	7.8	5.9	7.0	6.6	10.6	10.0	7.8	—	—
n	3 973	3 841	3 336	2 796	4 839	4 174	4 998	2 779	972	1 116	1 155	452	398

[1]) Age data from samples taken during experimental fishing.

Table 6 (cont.).

Year / Age	1963	1964	1965	1966	1967	1968	1969	1970	1971	1972[1])	1973[1])	1974[1])
2	—	—	—	—	—	—	—	—	—	—	0.2	6.7
3	—	0.2	—	—	—	—	—	0.3	0.6	44.1	5.1	2.0
4	6.9	5.9	5.2	0.1	0.2	—	0.1	1.8	3.3	19.5	83.7	7.3
5	0.4	60.6	13.6	8.8	0.4	0.7	—	0.4	4.4	13.1	2.8	82.0
6	0.4	0.3	66.3	28.9	12.8	1.3	3.3	0.6	1.8	9.1	4.1	0.9
7	0.5	0.1	0.1	54.5	33.7	12.1	0.8	4.4	4.9	2.2	1.7	0.8
8	1.7	0.2	0.2	0.2	48.5	35.0	13.2	1.3	5.1	4.2	0.8	0.2
9	1.0	0.8	0.1	0.1	0.2	47.7	38.2	17.0	1.7	0.9	0.6	—
10	8.6	0.5	0.3	0.1	—	0.1	41.6	35.2	20.9	0.1	0.9	0.1
11	3.6	3.4	0.5	0.2	0.1	—	—	37.9	32.1	2.3	+	—
12	8.2	1.8	1.4	0.2	0.3	0.2	0.3	0.1	25.0	2.3	+	—
13	60.0	2.6	0.8	0.6	0.2	0.2	0.1	0.1	—	2.2	+	—
14	2.0	20.9	1.3	0.6	0.5	0.3	0.3	0.1	+	—	+	—
15	2.7	0.6	9.2	0.4	0.3	0.5	—	0.1	—	—	+	—
16	2.0	0.7	0.3	5.0	0.3	0.4	0.2	0.1	+	—	+	—
17	0.8	1.1	0.3	—	2.5	—	0.3	0.2	+	—	—	—
18	0.5	0.1	0.3	—	—	1.4	0.1	0.2	+	—	—	—
19	0.4	0.1	—	0.3	—	—	1.3	—	+	—	—	—
20	0.2	0.1	—	—	—	—	—	0.3	—	—	—	—
21	—	—	0.2	—	—	—	—	—	+	—	—	—
22	—	—	—	—	—	—	—	—	—	—	—	—
23	0.1	—	—	—	—	—	—	—	—	—	—	—
?	—	—	—	—	—	—	—	—	—	—	—	—
n	399	1 481	1 402	2 531	1 599	2 255	2 207	3 511	2 516	856	1 994	2 178

result of the escalation in the summer and autumn fishery off Iceland where the catch reached a peak about 1 million tonnes in 1966 (Anon. 1972).

The method used for estimating the spawning stock size is liable to errors in the age composition of the winter herring fishery, especially when strong year classes younger than 7 years old are present in the spawning stock. This was the case in the years 1954—1956 and 1963—1965.

After comparing the age composition of the winter herring fishery with the age composition of the total stock calculated by VPA, the estimates show that for the 1950 year class 16% of the 4 years old, 47% of the 5 years old, and 60% of the 6 years old fish spawned. For the 1959 year class the figures are 3%, 63% and 100% respectively.

There is an increasing trend in fishing mortality with age in the adult stock. This is illustrated in Fig. 4 where mean fishing mortalities of the age groups 7—9, 10—12 and 13—15 years are plotted for the period 1950—1965. In the period 1956—1965 the fishing mortality is consistently

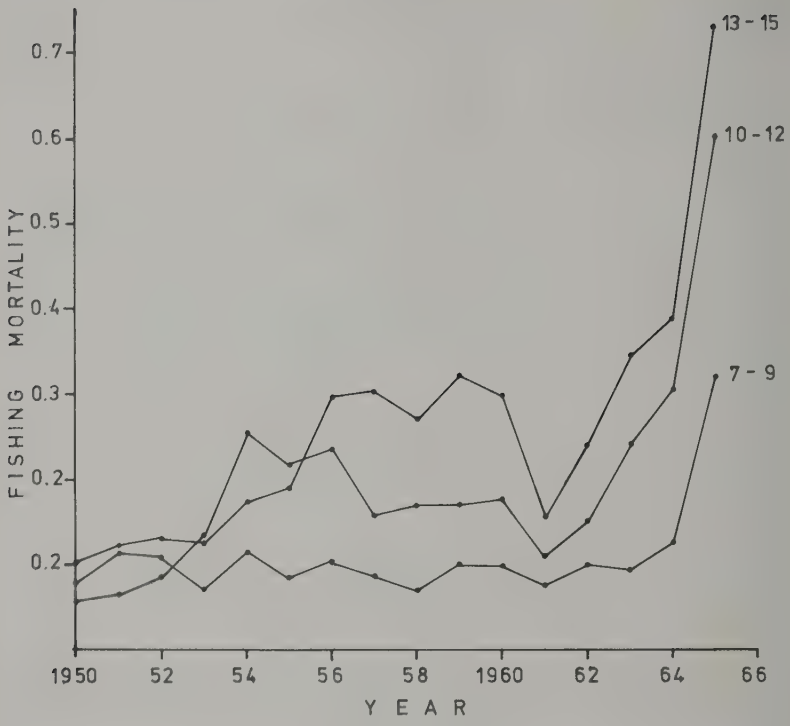

Fig. 4. Mean fishing mortality on 7—9, 10—12 and 13—15 years old herring 1950—1965.

at a minimum for the age groups 7—9 and at a maximum for those of 13—15 years. The oldest age group used in the VPA is the 20 years old herring, and the difference illustrated in Fig. 4 can therefore hardly be explained by the fishing mortalities assumed for the oldest age groups used in the VPA.

There may be several explanations for the observed increase in the fishing mortalities with age.

Two possible explanations are indicated:

1) The exploitation rate on old herring may have been higher than on younger herring in the summer and autumn fishery as indicated by an observed difference in age composition between the winter fishery and the summer and autumn fishery, especially in the 1950s (Fridriksson 1963, Devold 1963). It is interesting to note that the catches in the summer and autumn fishery show a significant increase around 1955,

Table 7. Fishing mortality by year class and age of young herring 1950—1969. The figures in brackets are uncertain because of the information for the VPA being from only a few years catches.

Age	Year class									
	1950	1951	1952	1953	1954	1955	1956	1957	1958	1959
0	0.058	0.07	0.75	0.35	1.12	0.92	0.73	0.80	1.38	0.30
1	0.11	0.64	0.66	0.91	1.06	1.18	1.45	1.59	1.27	0.37
2	0.023	0.07	0.21	0.14	0.67	0.34	1.52	0.78	0.91	0.12
3	0.016	0.04	0.03	0.04	0.04	0.04	0.10	0.73	0.15	0.10
Total	0.21	0.82	1.65	1.43	2.89	2.48	3.80	3.90	3.71	0.89

Table 7 (cont.)

Age	Year class									
	1960	1961	1962	1963	1964	1965	1966	1967	1968	1969
0	0.35	0.45	0.79	0.22	0.26	1.17	0.28	0.46	1.32	0.50
1	0.92	0.58	1.62	0.18	0.44	1.38	2.63	1.18	2.36	(1.28)
2	0.12	0.62	0.69	0.28	0.34	0.47	0.93	1.96	(1.41)	(0.68)
3	0.12	0.06	0.65	0.31	0.50	3.26	1.98	(0.41)	(0.22)	(0.60)
Total	1.51	1.71	3.75	0.98	1.53	6.28	5.82	(4.01)	(5.31)	(3.06)

i. e. at the same time as the observed increase in fishing mortalities with age began.

2) Another possibility is that natural mortality increases with age. In the VPA the natural mortality is assumed constant; if, however, it increases with age, it will show up in the calculations as increasing fishing mortalities.

YOUNG HERRING

Table 7 shows the fishing mortality of the age groups 0—3 for the year classes 1950—1969, and Table 8 shows the year class size in number at different ages. The year class size of 0-group and 4 years old herring are plotted in Fig. 5.

The exploitation rate on young herring was high during the whole period of 1950—1969. From Fig. 5 and Table 8 it can be seen that there is clear correlation between year class size and survival during the young herring stages. The survival rate decreases with decreasing year class

Table 8. Stock size in numbers ($N \times 10^{-6}$) of young herring by year class and age and survival (S) from 0-group to 4 years old 1950—1969. The figures in brackets are uncertain because of the information for the VPA being from only a few years catches.

Age	Year class									
	1950	1951	1952	1953	1954	1955	1956	1957	1958	1959
0	97 375	26 081	27 910	20 973	16 878	9 188	11 098	9 725	13 723	74 965
1	78 267	20 718	11 254	12 642	4 680	3 114	4 558	3 723	2 937	47 442
2	59 690	9 289	4 969	4 330	1 377	816	906	644	702	27 965
3	49 721	7 380	3 448	3 220	600	494	169	252	241	21 175
4	41 687	6 043	2 852	2 637	490	405	130	103	176	16 297
S	0.428	0.232	0.102	0.126	0.029	0.044	0.012	0.011	0.013	0.217

Table 8 (cont.).

Age	Year class									
	1960	1961	1962	1963	1964	1965	1966	1967	1968	1969
0	47 478	18 327	7 242	26 264	17 305	3 560	17 334	1 245	2 587	1 515
1	28 631	9 927	2 807	17 957	11 426	942	11 194	669	589	(782)
2	9 751	4 754	475	12 792	6 297	201	682	175	(47)	(185)
3	7 337	2 175	203	8 281	3 832	107	230	(21)	(10)	(80)
4	5 552	1 747	91	5 185	1 987	4	(27)	(12)	(7)	(38)
S	0.117	0.095	0.013	0.197	0.115	0.001	(0.002)	(0.010)	(0.003)	(0.025)

strength. This is illustrated in Fig. 6 where the logarithm of the number (ln N) is plotted against age for two weak year classes (1955 and 1962) and two strong year classes (1950 and 1959). Year classes, recorded in the 1950s, which traditionally have been called weak, were all, compared to the results presented in Fig. 5, of what could be called an ordinary strength of 10×10^9 – 30×10^9 fish at the 0-group stage. However, year classes of strengths less than 20×10^9 as 0-group survived the fishery only in small quantities to reach the age of 4 years. In addition to the year classes of ordinary strength there were three extraordinarily strong year classes (those of 1950, 1959 and 1960). The 1965 year class (or possibly that of 1962) was the first one in the period studied which really should ble classified as weak.

The decreasing survival rate with year class strength indicates that the same fishing effort in a purse seine fishery, such as that for young herring

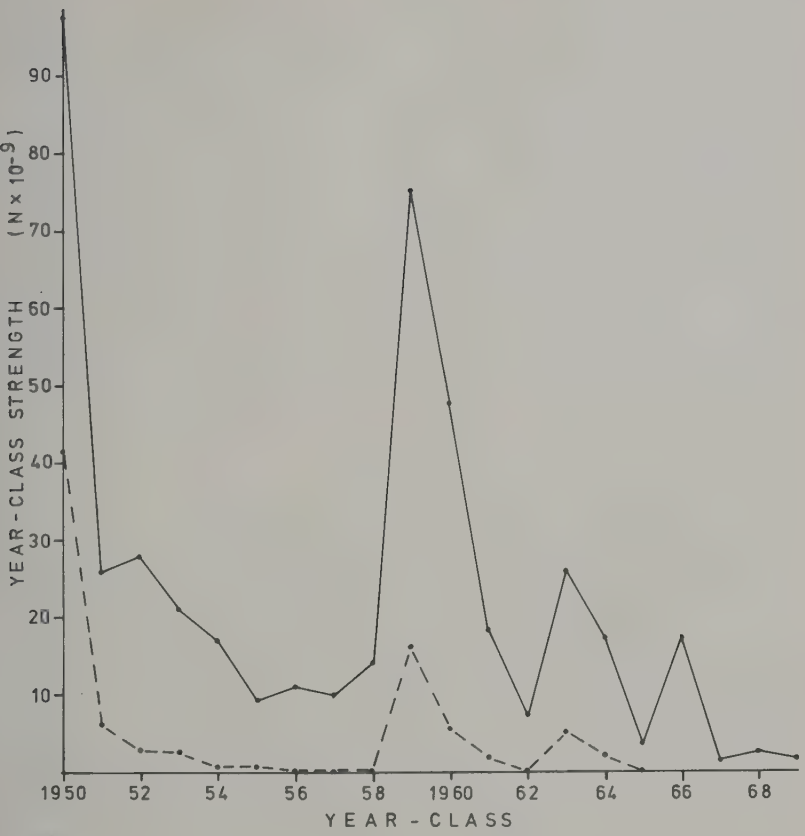

Fig. 5. Year class strength in number as 0-group and 4 years old (broken line) 1950—1969.

going on in coastal waters, may generate a much higher fishing mortality when stock abundance is low than when the abundance is higher. However, it also reflects that strong year classes had a more offshore distribution, and that part of those year classes therefore were outside the traditional fishing areas (Dragesund and Nakken 1973).

The 1961 year class was the last one which recruited to the spawning stock in any quantity (Table 6). It can be seen from Fig. 5 and Table 8 that some herring of the relatively strong 1963 and 1964 year classes survived to an age of 4 years. The portions of these two year classes which survived the fishery during the first years of life were, however, practically fished out in the fat-herring fishery in 1968 going on off the Finnmark coast. The VPA for that year gives fishing mortality estimates as high as 4.5 (Table 5). The

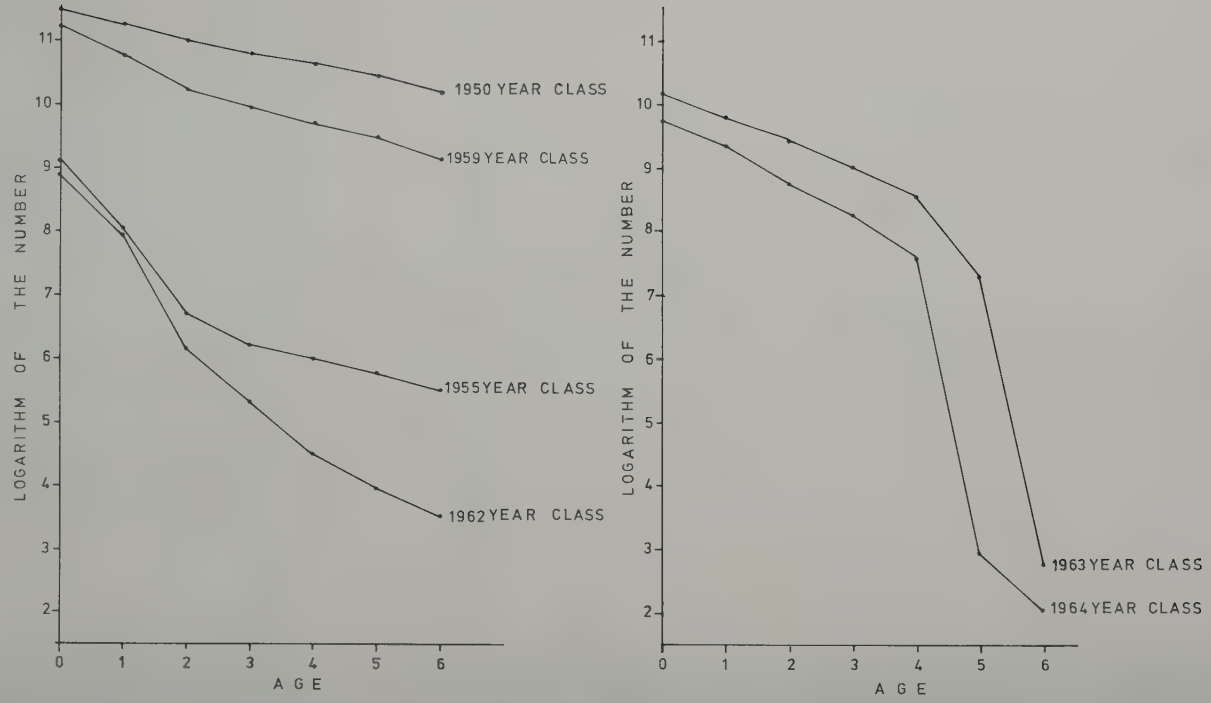

Fig. 6. Logarithm of the number against age for selected year classes.

mortality of these two year classes at different ages is also illustrated in Fig. 6 where ln N is plotted against age.

At the 0-group stage the 1964 and 1966 year classes were of approximately the same strength (Table 8, Fig. 5). However, the 1966 year class was practically fished out in the small-herring fishery in 1967 which generated a fishing mortality of 2.6 in that year (Table 7). When the 1967–1969 year classes were at the 0-group stage, they were of the order of only 10% of the 1963, 1964 and 1966 year classes (Table 8), and the 1969 year class was the only one which was observed in the spawning stock in any quantities the years 1973—1975.

The VPA gives no reliable estimates of the strength of the 1970—1972 year classes, but they were all very weak, tentatively of the order of 10% of the 1967—1969 year classes, i. e. of the order of only 1% of the 1963, 1964 and 1966 year classes.

CONCLUDING REMARKS

The serious effect of the young herring fishery on the recruitment to the adult stock is clearly illustrated in Fig. 5. Even in the 1950s a year class apparently had to be of a size of about 20×10^9 in number as 0-group if a significant quantity was to have a chance to escape the small- and fat-herring fisheries. This means a year class strength of 2–3 times the average strength for the North Sea herring stock which has been estimated to be able to sustain an annual yield of about 800 thousand tonnes if properly managed (Anon. 1973). All year classes in the period 1950—1966, except those of 1962 and 1965, would probably have recruited the adult stock in at least the same quantity as the very strong 1960 year class did if they had not been fished as juveniles.

The 1963 and 1964 year classes were the last ones which survived to an age of 4 years in any quantity, but these two year classes were practically fished out in the fat-herring fishery in 1968 (Table 5, Fig. 6). Dragesund and Ulltang (1972, 1973) discussed the possibility that increased natural mortality from 1968 onwards increased the rate of decline in the adult stock. The authors still regard this as a possibility, and it is also possible that some more fish of the 1963 and 1964 year classes, which never showed up in the spawning stock because of increased natural mortality, were left after 1968. Fishing mortalities of about 4.5, as estimated for these two year classes in 1968, mean that only 1% of the fish present at the beginning of the year survived the fishery, and this seems unlikely as the year classes in question had an offshore distribution in 1968.

The results of the present investigation leave, however, no doubt that the fishing pressure, especially on young and adolescent herring and also on adult herring in the years 1965—1968, was the primary factor for the

collapse of this herring stock. A possible increased natural mortality in later years may have been the result of the already extremely low stock size. In the same way as the fishing fleet was able to generate a much higher fishing mortality on weak than on strong year classes, as demonstrated in Fig. 6 and Table 7 and 8, the predators may have been able to generate a much higher natural mortality when the stock was so strongly depleted by the fishery.

It seems evident from Fig. 3 and 5 that the collapse could have been a reality at a much earlier stage if it had not been for the extraordinarily strong year classes of 1950, 1959 and 1960.

The weak year classes from 1967 onwards were probably the result of the low spawning stock size. If the decline in spawning stock size in 1967 reached the critical level where there is a clear relationship between spawning stock biomass and subsequent recruitment, it means that this critical level for the Norwegian spring spawning herring may be of the order of 1—2 million tonnes. The spawning stock size of 1967 was estimated to 1.3 million tonnes, or 0.8 when catch in the winter fishery is subtracted. The lowest level ever recorded earlier in the period studied, was 1.6 million tonnes in 1963, or 1.5 when catch in the winter fishery is subtracted, and the 1963 year class was relatively strong.

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SURVIVAL OF TAGGED BARENTS SEA CAPELIN (*MALLOTUS VILLOSUS* MÜLLER) AND ESTIMATES OF THE 1973, 1974 AND 1975 SPAWNING STOCKS FROM TAG RETURNS

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ABSTRACT

DOMMASNES, A. 1978. Survival of tagged Barents Sea capelin (*Mallotus villosus*, Müller) and estimates of the 1973, 1974 and 1975 spawning stocks from tag returns. *FiskDir. Skr. Ser. HavUnders.*, *16* : 339—358.

Capelin tagged with internal stainless steel tags were kept in net enclosures for 8—9 days to obtain the survival factor. This was found to be 0.89 for males while additional information from routine tag recoveries indicated a survival factor of 0.51 for females.

The 1973 spawning stock was calculated separately from two different groups of tagged fish released at different times during the fishery. The resulting estimates were 2.2 and 4.1 million metric tonnes.

The 1974 spawning stock was calculated from three tagging experiments. The resulting estimates were 5.8, 1.1 and 1.9 million tonnes. The highest value is rejected as being obviously too high.

The 1975 spawning stock was calculated from two tagging experiments. Both gave an estimate of 1.1 million tonnes.

Some possible causes of error in the estimates are discussed.

INTRODUCTION

The Institute of Marine Research has carried out tagging of capelin with internal stainless steel tags since 1970, mostly during the winter fisheries on capelin migrating to the coast of Finnmark for spawning. The tags are recovered in fish meal factories by means of magnets in the production line and during cleaning of the machinery.

Tagging with internal metal tags and recovery by magnets was first described by ROUNSEFELL and DAHLGREN (1933). The method was later used successfully on herring (FRIDRIKSSON and AASEN 1950, 1952; AASEN 1958; DRAGESUND & HARALDSVIK 1966; ANON. 1975) and on mackerel (HAMRE 1975).

Abundance estimates of the 1971 and 1972 spawning stocks of Barents Sea capelin from tag returns have been published by DRAGESUND, GJØSÆTER and MONSTAD (1973).

Little knowledge is available on the survival of tagged capelin. DRAGESUND, GJØSÆTER and MONSTAD (1973) used 0.80 as an estimate of the survival factor for both females and males. Lack of information about survival has been one of the factors that seriously reduced the reliability of stock estimates based on tag returns. It was therefore decided to carry out a test experiment during the winter capelin fishery in 1974 to obtain more knowledge about the survival of tagged capelin.

THE SURVIVAL FACTOR

THEORY

The survival of tagged and untagged fish in the test can be expressed as follows:

$$S_1 = N_1 \cdot e^{-(M + T_1 + T_2 + L) \cdot t}$$

$$S_2 = N_2 \cdot e^{-(M + T_2) \cdot t}$$

or:

$$\frac{S_1}{S_2} = \frac{N_1}{N_2} \cdot e^{-(T_1 + L) \cdot t}$$

N_1 = number of tagged fish at the start of the test
N_2 = number of untagged fish at the start of the test
S_1 = number of tagged fish that survive without losing the tag
S_2 = number of untagged fish that survive
M = instantaneous natural mortality
T_1 = instantaneous mortality caused by the tagging operation
T_2 = instantaneous mortality caused by the handling apart from the tagging operation
L = instantaneous loss of tags (shedding)
t = time interval

Denoting $e^{-(T_1 + L) \cdot t}$ the tagging survival factor (s) we have:

$$s = \frac{S_1 \cdot N_2}{S_2 \cdot N_1} \qquad \text{(I)}$$

The estimate of s obtained in this way includes the mortality caused by the tagging operation and the loss of tags up to time t. The estimate according to (II) is thus to be regarded as an overestimate, partly due to eventual limitation in t, and partly due to mortality caused by the handling apart from the tagging operation.

MATERIAL AND METHODS

The test was carried out in Nordvågen, approximately 7 kilometers east of Honningsvåg, in February and March 1974.

The capelin used in the experiments were caught by purse seine approximately 60 nautical miles off the coast. After capture the fish were transferred to two tanks (each approx. 1.5 m^3) on the deck of the vessel. The tanks were continously supplied with seawater from a pump. Transport to the site of the experiment took 16 hours. The position of capture and of the test site are indicated in Fig. 3.

Tagging took place at the test site and was done according to the same procedure as in the open sea. The fish were taken one by one from the storage tanks with a dip net, and the tag was inserted by hand. No tagging gun, scalpel or other equipment was used, the tag being pressed into the body cavity without any sectioning in advance. This seems to cause the smallest wound. The tag was always inserted on the left side, slightly anterior to the anus (Fig. 1). After the tag had penetrated the body wall, it was turned so that it pointed straight forward, and then pushed completely into the abdominal cavity. Only fish larger than 15 cm were used. The tags, in lots of 50, were put into a jar of alcohol before use, and were picked out from there just before being inserted. As a result, both the tags and the fingers that came in contact with the wound were sterilized.

The tagged fish were collected in buckets and released into the net enclosures in batches of 10—25 fish.

The dimensions of the standard stainless steel capelin tags are 14 × 3 × 0.3 mm (Fig. 1).

The tagged fish and an equal number of untagged capelin were released into two net enclosures approximately 3.4 × 3.4 m at the surface and approximately 3.4 m deep. The surfaces of the enclosures were covered by nets. A 25 W electric lamp was placed in each enclosure to enable the fish to see the net wall. Into one enclosure 400 tagged and 400 untagged fish were released (Experiment 1), into the other 300 tagged and 300 untagged fish (Experiment 2). The surface temperature was 3.2°C where the fish were caught and 2.2°C at the experiment site.

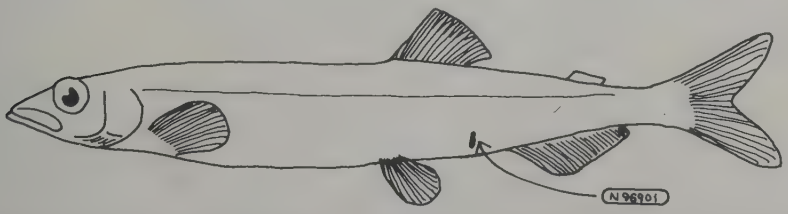

Fig. 1. A capelin. The position where the tag is pushed into the abdomen is indicated by an arrow. A tag is shown in correct relative size.

Dead fish were scooped up with a dip net twice on the first day after the experiment started and every morning on the other days. The dead fish were examined for tags, measured, and sex and maturity were noted. All tagged fish had the position of the tag noted if still present. Loss of the tag was also noted. At the end of the test all remaining fish were scooped up, and the same information recorded. The sex was not noted before the fish were released into the enclosures.

RESULTS AND DISCUSSION

At the end of the test some fish were missing: in «Experiment 1» 29 tagged and 5 untagged fish; in «Experiment 2» 79 tagged and 77 untagged fish. There seem to be several reasons for the loss of fish. Some fish were taken by kittywakes *(Rissa tridactyla)* as they were released into the enclosures, before the cover net was in position. According to observers ashore others were taken by eider ducks *(Somateria mollissima)*. On two occasions corners of the cover net were torn loose by waves and wind so that it may have been possible for the ducks to dive into the enclosures. There were often large flocks of eider ducks around the test site. At the end of the test it was also found that one corner of the second enclosure («Experiment 2») where an anchor rope was fastened had been pulled under the surface by the current. At the same time the cover net had been pulled loose. This is probably the main reason why so many fish disappeared from «Experiment 2».

The three first series (50 fish in each series) of tagged fish in «Experiment 1» had very high mortality the first 20 hours. Most of them seemed to die immediately after release into the enclosure. This was probably due to lack of oxygen in the bucket where the fish were kept between tagging and release.

For the first three series about 25 fish were put into the bucket before they were transferred to the net enclosure. Later no more than 10 fish were collected in the bucket before transfer. For untagged fish the transfer probably did not create problems as it was much quicker for them. For all calculations except the tag retainment factor the three first series in «Experiment 1» have been disregarded. The remaining tagged fish in «Experiment 1», together with the 400 untagged fish in that enclosure, will be referred to as «Experiment 1a».

The results (Tables 1 and 2) show a very high mortality for both tagged and untagged females, much higher than for males. It is not possible from these results to calculate any reasonable value of the survival factor for females. The results give reason to suspect that for females the mortality from other factors than the tagging operation is so large that it obscures the tagging mortality.

Table 1. Results of Experiment 1a.

Experiment 1a	Date	Time	Tagged			Untagged		
			♀	♂	♀+♂	♀	♂	♀+♂
Released into net enclosures	20 Feb.	13.05—14.35	58[1])	192[1])	250	104[1])	296[1])	400
Recovered dead	21 Feb.	09.00	32	12	44	49	9	58
» »	21 »	16.00	5	4	9	10	5	15
» »	22 »	09.00	2	5	7	8	4	12
» »	23 »	09.15	7	2	9	11	7	18
» »	24 »	09.30	1	3	4	4	2	6
» »	25 »	09.30	2	1	3	2	2	4
» »	26 »	10.15	2	3	5	4	3	7
» »	27 »	09.10	0	2	2	6	12	18
» »	28 »	08.50	2	3	5	3	1	4
Total number of dead during experiment			53	35	88	97	45	142
Surviving fish recovered at end of experiment.....	28 Feb.	09.10	1	145	146	6	247	253
Total number of fish recovered			54	180	234	103	292	395
Total number of fish lost			4[1])	12[1])	16	1[1])	4[1])	5
Tag retainment factor[2])			—	0.95				
Surviving fish recovered retaining the tags[3])			—	145				

[1]) The numbers have been estimated on the assumption that the sex ratio among fish released was the same as among those recovered.

[2]) The tag retainment factor has been calculated from the complete «Experiment 1».

[3]) This number has been calculated using the tag retainment factor.

Table 2. Results of Experiment 2.

Experiment 2	Date	Time	Tagged			Untagged		
			♀	♂	♀+♂	♀	♂	♀+♂
Released into net enclosures	20 Feb.	15.45—17.45	45[1])	255[1])	300	56[1])	244[1])	300
Recovered dead	21 Feb.	09.30	15	5	20	14	2	16
» »	21 »	16.00	3	6	9	11	1	12
» »	22 »	08.15	4	7	11	8	2	10
» »	23 »	09.00	3	2	5	4	3	7
» »	24 »	09.20	2	0	2	0	1	1
» »	25 »	09.00	2	4	6	2	2	4
» »	26 »	10.10	2	6	8	1	3	4
» »	27 »	09.00	1	5	6	1	3	4
» »	28 »	09.30	1	0	1	0	1	1
» »	1 March	08.30	0	4	4	0	2	2
Total number of dead during experiment			33	39	72	41	20	61
Surviving fish recovered at end of experiment.....	1 March		0	149	149	1	161	162
Total number of fish recovered			33	188	221	42	181	223
Total number of fish lost			12[1])	67[1])	79	14[1])	63[1])	77
Surviving fish recovered retaining the tags			0	145				
Tag retainment factor			—	0.97				

[1]) The numbers have been estimated on the assumption that the sex ratio among fish released was the same as among those recovered.

TAGGING SURVIVAL FACTOR FOR MALE CAPELIN, $s\sigma$

In order to determine the numbers of each sex that were released into the net enclosures at the start of the experiment it was assumed that the sex ratio among the fish that were released was the same as for those recovered, and that mortality was the same among fish lost as among those recovered. The corresponding values of S_1, N_1, S_2 and N_2 are given in Table 3b, combination A. Using formula (I), «Experiment la» gives $s\sigma = 0.91$ and «Experiment 2» gives $s\sigma = 0.87$. The mean value is 0.89.

The most obvious sources of error in these estimates are the assumptions of the sex ratios of the fish originally released into the enclosures, and the theories of what happened to the lost fish. In Tables 3a and 3b are listed some other possible assumptions and the resulting values of S_1, N_1, S_2, N_2 and $s\sigma$. The lowest value of $s\sigma$, 0.85, is obtained from assumption *E* in «Experiment la». The highest value, 0.92, is obtained from several of the assumptions.

It is reasonable to assume that if all the fish that were released could have been accounted for, the test would still have given a value of $s\sigma$ somewhere between the above mentioned extremes. It is also probable that small variations in the handling and tagging technique, as are likely to occur if the tagging is done by different people, may cause the survival factor to change beyond the extremes calculated. This was demonstrated in the report from the ICES Working Group on the Bløden Tagging experiment 1969/70 (ANON. 1975) where two tagging teams were used, and it was found that the mean recapture rate of fish tagged by team 2 relative to team 1 was 0.73. It must be further remembered that $s\sigma$ only represents a maximum value for the tagging survival factor, because it does not take into account mortality due to stress from the catching procedure or the stay in the storage tanks.

Table 3a. Some possible combinations ot sex ratio and mortality of the lost fish.

A The sex ratios among the fish initially released into the enclosures was the same as among those recovered, and the ratio dead/survivors was the same among those lost as among those recovered in the groups «tagged» and «untagged», respectively.

B The sex ratios among the fish initially released into the enclosures was the same as among those recovered, and all lost fish are considered as survivors.

C The sex ratios among fish initially released into the enclosures was the same as among those recovered, and all lost fish are considered as dead.

D All lost fish are considered as surviving males.

E All lost fish are considered as dead males.

F All lost fish are considered as females.

Table 3b. Values of S_1, N_1, S_2, N_2 and $s\sigma$ for the combinations of sex ratio and mortality given in Table 3a. Loss of tags has been included in s, using the «Tag retainment» factors given in Tables 1 and 2.

	Experiment 1a					Experiment 2				
	N_1	S_1	N_2	S_2	$s\sigma$	N_1	S_1	N_2	S_2	$s\sigma$
A	192	147	296	250	0.91	255	197	244	217	0.87
B	192	149	296	251	0.92	255	210	244	218	0.92
C	192	138	296	247	0.86	255	145	244	161	0.86
D	196	153	297	252	0.92	267	222	258	238	0.90
E	196	138	297	247	0.85	267	145	258	161	0.87
F	180	138	292	247	0.91	188	145	181	161	0.87

THE SIZES OF THE SPAWNING STOCKS

THEORY

When calculating the size of the capelin population based on tagging, the Petersen method was used (RICKER 1975):

$$\hat{V} = \frac{C \cdot N \cdot s}{R} \qquad \text{(II)}$$

$\hat{V}$ = estimate of population at time of tagging,
C = size of catch after tagging in the same unit as $\hat{V}$,
N = number of fish tagged,
s = «tagging survival factor» which must also take into account loss of tags (shedding),
R = number of tags recovered.

When the sex of the tagged fish is known, the calculations are based on male fish only. If one assumes that the proportion of male capelin in the catches ($k\sigma$) is the same as in the spawning population, one can write:

$$\hat{V} \cdot k\sigma = \frac{C \cdot k\sigma \cdot N\sigma \cdot s\sigma}{R\sigma}$$

$$\hat{V} = \frac{C \cdot N\sigma \cdot s\sigma}{R\sigma} \qquad \text{(III)}$$

An estimate of the total spawning population ($\hat{P}$) disregarding natural mortality in the period concerned is found from the formula

$$\hat{P} = C_0 + \hat{V} \qquad \text{(IV)}$$

where C_0 is the catch taken before the tagged fish were released.

When the ratio $\frac{R}{C}$ is small, the standard deviation of the inverse value of V (RICKER 1975) is:

$$\text{St. dev.}\left(\frac{1}{V}\right) = \frac{\sqrt{R}}{C \cdot N \cdot s} \qquad \text{(V)}$$

Using (II) and (V) one obtains the 95% limits of confidence for $\left(\frac{1}{V}\right)$:

$$\frac{R - 1.96 \cdot \sqrt{R}}{C \cdot N \cdot s} < \frac{1}{V} < \frac{R + 1.96 \cdot \sqrt{R}}{C \cdot N \cdot s}$$

Inverting the values and introducing (IV) gives the 95% confidence limits for P:

$$C_o + \frac{C \cdot N \cdot s}{R + 1.96 \cdot \sqrt{R}} < P < C_o + \frac{C \cdot N \cdot s}{R - 1.96 \cdot \sqrt{R}} \qquad \text{(VI)}$$

or, adapted to (III):

$$C_o + \frac{C \cdot N_{\sigma} \cdot s_{\sigma}}{R_{\sigma} + 1.96 \cdot \sqrt{R_{\sigma}}} < P < C_o + \frac{C \cdot N_{\sigma} \cdot s_{\sigma}}{R_{\sigma} - 1.96 \cdot \sqrt{R_{\sigma}}} \qquad \text{(VII)}$$

MATERIAL AND METHODS

In order to calculate the spawning population the fish tagged in 1973 were divided into two groups, and calculations were made for each group separately. In 1974 three groups were used, in 1975 two groups.

In 1973 no attempt was made to determine the sex of the tagged fish, and the first 1000 fish tagged in 1974 were not sexed either. Later, each series of 50 tags was used for one sex only. The sex was determined from external characters.

The time of release for each group of tagged fish and the number of fish released is shown in Tables 4, 5 and 6 for 1973, 1974 and 1975, respectively. The areas of release are shown in Figs. 2, 3 and 4.

The input data used in the calculations were obtained as follows:

C_o was obtained from the catch statistics as the total catch fished before the date when the first tagged fish in the group were released. R and the corresponding C were obtained from plants that had a magnet efficiency coefficient above 0.40 in 1973, and above 0.50 in 1974 and 1975.

Table 4. Release dates and numbers of tagged capelin released in 1973.

	Date	Numbers released (Sex not determined)
	27 Feb.	1 500
	1 March	1 400
Group 1	2 »	1 000
	6 »	950
	8 »	150
Group 2	21 »	2 000
	22 »	1 500

Table 5. Release dates and numbers of tagged capelin released of each sex in 1974.

	Date	Numbers released		
		Sex not determined	♀	♂
Group 1	19 Feb.	1 000		
	11 March		1 000	1 000
	12 »		1 000	1 000
Group 2	13 »		1 000	1 000
	14 »		500	500
	15 »		500	500
	19 March		250	250
Group 3	20 »		900	600
	21 »		700	300
	25 »		1 000	500

Table 6. Release dates and numbers of tagged capelin released of each sex in 1975.

	Date	Numbers released	
		♀	♂
Group 1	8 March	500	1 000
	9 »		1 500
	15 March		2 000
Group 2	16 »		1 500
	17 »		1 000
	18 »		500

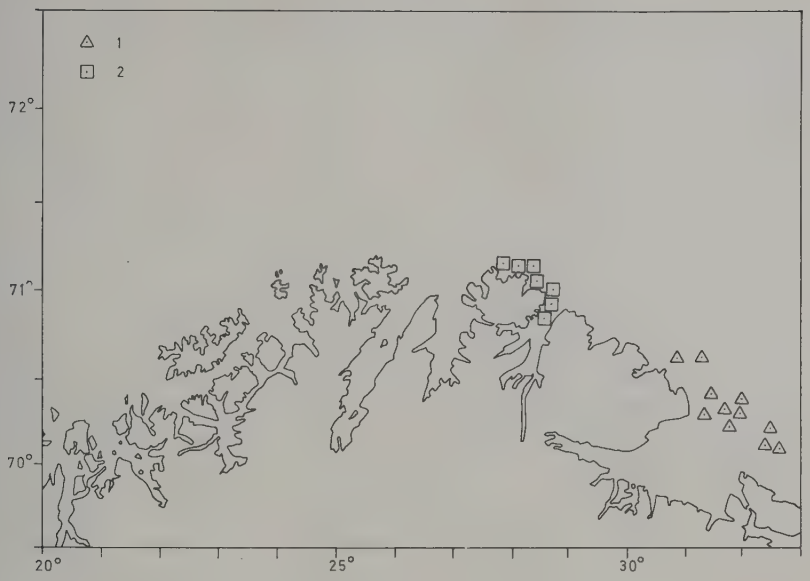

Fig. 2. Positions where tagged capelin were released in 1973.
1) Group 1, 2) Group 2.

The magnet efficiency coefficient, which is the proportion of retained tags to the number of tags in the catch produced, was determined by tagging in the usual way, but with unnumbered tags and «releasing» on the conveyor belt of the meal plant concerned. Of the 6 factories tested in 1973, 5 had magnet efficiency coefficients above 0.40. From one of these, however, no numbered tags were recovered and it too has been omitted from the calculations. In 1974, 12 factories were tested, and 7 had coefficients above 0.50. In 1975, 8 factories were tested, and 5 had coefficients above 0.50. The relevant values of R and the corresponding corrected catch C are shown in Tables 7, 8 and 9.

Where only tags from male capelin were used, the survival factor $s♂ = 0.89$ was employed. For the 1973 material, where the sex of the tagged fish is not known, samples from the same area and time period indicate a sex ratio of 62% females to 38% males. Assuming a survival factor for females $s♀ = 0.51$ (to be discussed later), a weighted value of $s = 0{,}65$ is obtained for the 1973 material. For group 1, 1974, samples indicate a sex ratio of 50 % females and 50% males, and a survival factor $s = 0.70$ has been used.

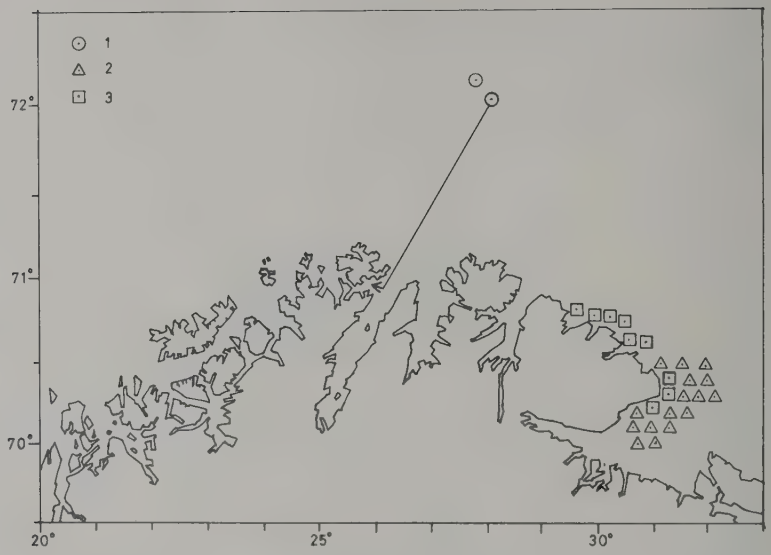

Fig. 3. Positions where tagged capelin were released in 1974.
1) Group 1, 2) Group 2, 3) Group 3. The line indicates the transport of live capelin that were used in the tagging survival experiment.

RESULTS AND DISCUSSION

1973

Equations (II) and (IV) were used for calculation of the spawning population, and the 95% confidence interval was calculated from (VI). The input data used in the formulas are summarized in Table 10 and give the following results:

Group 1

Population estimate: $\hat{P} = 2.18 \times 10^6$ tonnes

Confidence interval: 1.93×10^6 tonnes $< P < 2.52 \times 10^6$ tonnes

Group 2

Population estimate: $\hat{P} = 4.12 \times 10^6$ tonnes

Confidence interval: 3.12×10^6 tonnes $< P < 6.54 \times 10^6$ tonnes

Table 7. Tag return efficiencies for the factories in 1973, quantities delivered to the factories after the tags were released (in metric tonnes), corrected quantities, returned tags and returned tags per 10 000 tonnes corrected quantity. Note that the designations A, B, C, ... do not cover the same factories each year.

Factory	Tag return efficiency	Group 1				Group 2			
		Quantity tonnes	Corrected quantity	Returned tags		Quantity tonnes	Corrected quantity	Returned tags	
				Total	per tonne $\times 10^4$			Total	per tonne $\times 10^4$
A	.95	30 008	28 508	42	15	12 247	11 635	5	4
B	.74	20 100	14 873	41	28	9 240	6 837	12	18
C	.48	72 290	34 698	48	14	22 543	10 820	3	3
D	.41	18 390	7 540	22	29	8 253	3 384	2	6
Total ...			85 619	153			32 677	22	

1974

For 1974 the spawning population was calculated from (II) and (IV) for Group 1 and from (III) and (IV) for Groups 2 and 3. The 95% confidence interval was calculated from (VI) for Group 1 and from (VII) for Groups 2 and 3. The input data are summarized in Table 11:

Group 1
Population estimate: $\hat{P} = 5.78 \times 10^6$ tonnes
Confidence interval: 4.10×10^6 tonnes $< P < 9.89 \times 10^6$ tonnes

Group 2
Population estimate: $\hat{P} = 1.06 \times 10^6$ tonnes
Confidence interval: 1.00×10^6 tonnes $< P < 1.13 \times 10^6$ tonnes

Group 3
Population estimate: $\hat{P} = 1.96 \times 10^6$ tonnes
Confidence interval: 1.66×10^6 tonnes $< P < 2.45 \times 10^6$ tonnes

1975

For 1975 the spawning population was calculated from (III) and (IV) and the 95% confidence interval from (VII). The input data are summarized in Table 12:

Table 8. Tag return efficiencies for the factories in 1974, quantities delivered to the factories after the tags were released (in metric tonnes), corrected quantities, returned tags and returned tags per 10 000 tonnes corrected quantity. For Group 1 all tags returned from the factories in question have been used, for Groups 2 and 3 only tags from male fish. Note that the designations A, B, C, ... do not cover the same factories each year.

Factory	Tag return efficiency	Group 1				Group 2				Group 3			
		Quantity tonnes	Corrected quantity	Returned tags		Quantity tonnes	Corrected quantity	Returned tags		Quantity tonnes	Corrected quantity	Returned tags	
				Total	per tonne $\times 10^4$			Total	per tonne $\times 10^4$			Total	per tonne $\times 10^4$
A	.90	16 664	14 998	0	0	11 794	10 615	32	30	6 789	6 110	7	11
B	.81	21 625	17 516	2	1.1	16 218	13 137	50	38	7 079	5 734	5	9
C	.79	22 932	18 116	6	3.3	20 164	15 930	71	45	10 964	8 662	9	10
D	.78	95 807	74 729	3	0.4	53 801	41 965	172	41	27 166	21 189	22	10
E	.74	42 243	31 260	2	0.6	32 242	23 859	134	56	17 339	12 831	8	6
F	.61	21 081	12 859	5	3.9	17 086	10 422	52	49	7 658	4 671	6	13
G	.55	19 013	10 457	4	3.8	15 520	8 536	30	35	6 476	3 562	5	14
Total			179 935	22			124 464	540			62 759	62	

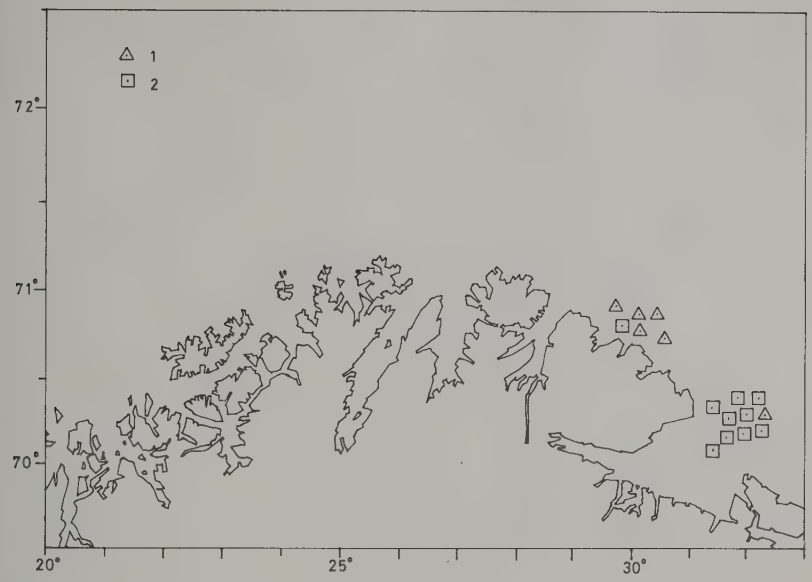

Fig. 4. Positions where tagged capelin were released in 1975.
1) Group 1, 2) Group 2.

Group 1

Population estimate: $\hat{P} = 1.14 \times 10^6$ tonnes

Confidence interval: 1.02×10^6 tonnes $< P < 1.29 \times 10^6$ tonnes

Group 2

Population estimate: $\hat{P} = 1.12 \times 10^6$ tonnes

Confidence interval: 1.04×10^6 tonnes $< P < 1.22 \times 10^6$ tonnes

A number of factors can have caused errors in the results. Some of these are discussed below.

The value used for the tagging survival factor is an obvious source of bias because it does not take into consideration the mortality caused by handling apart from the tagging operation. The actual tagging survival is therefore lower than indicated by s, and the population estimates given here must be regarded as overestimates.

A minimum requirement if a tagging experiment is to be used for calculating population sizes, is that the tagged fish must be randomly distributed in the population to be estimated or the fishing effort must be randomly distributed. If neither of these conditions is met, fishing mortality

Table 9. Tag return efficiencies for the factories in 1975, quantities delivered to the factories after the tags were released (in metric tonnes), corrected quantities, returned tags and returned tags per 10 000 tonnes corrected quantity. Only tags from male fish have been used. Note that the designations A, B, C, ... do not cover the same factories each year.

Factory	Tag return efficiency	Group 1				Group 2			
		Quantity tonnes	Corrected quantity	Returned tags		Quantity tonnes	Corrected quantity	Returned tags	
				Total	per tonne $\times 10^4$			Total	per tonne $\times 10^4$
A	.97	16 077	15 595	18	12	13 039	12 648	52	41
B	.78	10 076	7 849	12	15	9 358	7 299	100	137
C	.70	7 037	4 926	6	12	4 905	3 434	29	84
D	.69	69 385	47 876	143	30	47 237	32 594	128	39
E	.68	14 473	9 842	23	23	9 823	6 680	26	39
Total ...			86 098	202			62 655	335	

Table 10. Input data used to calculate the spawning stock in 1973.

	C_o (tonnes)	C (tonnes)	N	s	R
Group 1	362 033	85 619	5 000	.65	153
Group 2	739 426	32 677	3 500	.65	22

Table 11. Input data used to calculate the spawning stock in 1974.

	C_o (tonnes)	C (tonnes)	$N, N♂$	$s, s♂$	$R, R♂$
Group 1	58 433	179 935	1 000	.70	22
Group 2	238 495	124 464	4 000	.89	540
Group 3	469 246	62 759	1 650	.89	62

Table 12. Input data used to calculate the spawning stock in 1975.

	C_o (tonnes)	C (tonnes)	$N♂$	$s♂$	$R♂$
Group 1	190 609	86 098	2 500	.89	202
Group 2	283 672	62 655	5 000	.89	335

for the tagged fish is likely to be different from that of the whole population. In these experiments the tagged fish were released in batches in the areas where the fishing fleet was working. As a consequence, the first condition was probably not fulfilled. As to the second condition it is more difficult to say, but it was probably not fulfilled all the time.

The tag return efficiency was checked only once during the season for each factory. It is likely that efficiency is subject to some change during the season. This is indicated by the fact that there is considerable variation in the tag return efficiency for the same factory from year to year.

The two estimates for 1973 differ so much that their usefulness is seriously reduced, — 2.2 and 4.1 million tonnes, respectively. It is not possible from our material to tell whether the difference is due to one or more of the possible causes discussed above. It is therefore not really possible either to tell which of the two estimates is most correct. However, the lowest estimate is based on a higher number of released tagged fish and a larger catch. It therefore seems reasonable to put most emphasis on the lowest figure. On the other hand, an acoustic survey carried out in August 1972 resulted in an estimate of 3.7 million tonnes for the 1973 spawning stock (Nakken and Dommasnes 1975). This is closer to the highest estimate from the tagging experiments.

In the case of Group 1 1974, fishing mortality for the tagged fish must have been much lower than for the rest of the population. Immediately after the tagging a storm blew up and stopped the fishing almost completely for more than a week. After the storm this concentration of capelin could not be relocated, and fishing started in another area. Observations (Anon. 1974) also indicate that the capelin tagged in Group 1 1974 may have had very high natural mortality due to predation from cod. The extraordinarily high population estimate resulting from the tags in Group 1 should therefore be disregarded.

Having decided to disregard the population estimate from Group I 1974, one is left with the estimates from Groups 2 and 3. Again the estimates differ rather a lot — 1.1 and 1.9 million tonnes, respectively. In this case it also seems most reasonable to accept the lower estimate as the best one. This agrees quite well with an acoustic survey in September–October 1973 which resulted in an estimate of 1.0 million tonnes for the 1974 spawning stock, with a possibility that the value might be as high as 1.5 million tonnes (Nakken and Dommasnes 1975).

The estimates from Group 1 and Group 2 1975 both give a value of 1.1 million tonnes for the spawning stock. This does not exclude the possibility that both estimates may have been subject to error, but it still seems justifiable to put some confidence in the value. The acoustic survey in September–October 1974 resulted in an estimate of 0.8 million tonnes for the spawning stock in 1975 (Nakken and Dommasnes 1975).

The widely differing estimates of the 1973 and 1974 stocks using different groups of tags and the possibilities of error pointed out in the discussion suggest that stock estimates for capelin based on tagging experiments should be used with caution. Even so, they are in the same size range as the acoustic estimates and are useful for checking those figures.

TAGGING SURVIVAL FACTOR FOR FEMALE CAPELIN, $s♀$.

For most of the capelin tagged in 1974 and all capelin tagged in 1975, each series of 50 tags was used for one sex only. It is thus possible to calculate the ratio between returned tags and released tagged fish separately for the sexes. If one assumes that fishing mortality is the same for both sexes, different values of this ratio must be due to mortalities from other causes than fishing. Of those other causes, natural mortality is likely to be small compared to tagging mortality so that any difference in the ratios between returned and released tags can be assigned to different tagging mortality alone:

$$\frac{R♀}{N♀ \cdot s♀} = \frac{R♂}{N♂ \cdot s♂}$$

$$s♀ = s♂ \cdot \frac{N♂ \cdot R♀}{N♀ \cdot R♂} \qquad \text{(VIII)}$$

Table 13 shows the releases and recaptures by sexes for 1974 and 1975. Using these values and $s♂ = 0.89$ in equation (VIII) we get $s♀ = 0{,}51$ from the 1974 material and $s♀ = 0.59$ from the 1975 material. The 1975 sample is relatively small, and the 1974 estimate is therefore regarded as the most reliable one. Both samples confirm, however, the high tagging mortality for female capelin observed in the test experiments.

Table 13. Total numbers of capelin of each sex released in 1974 and 1975, and total numbers of tags returned.
$N♀$, $N♂$: numbers tagged
$R♀$, $R♂$: numbers of tage recovered.

Year	$N♀$	$N♂$	$R♀$	$R♂$
1974	6 850	5 650	644	931
1975	500	7 500	12	271

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DIFFERENTIATION BETWEEN «MARINUS» AND «MENTELLA» TYPES OF REDFISH BY ELECTROPHORESIS OF HAEMOGLOBINS

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ABSTRACT

NÆVDAL, G. 1978. Differentiation between «marinus» and «mentella» types of redfish by electorphoresis of haemoglobins. *FiskDir.Skr.Ser.HavUnders.*, *16* : 359–368.

Haemoglobins of 225 specimens of redfish from the Barents Sea and 357 specimens from Icelandic waters were analysed by electrophoresis to search for genetic differences between the morphologian *marinus* and *mentella* types. Two main haemoglobin patterns were commonly found, one characteristic for redfish of the *mentella* type and one characteristic for the *marinus* type. Specimens of *Sebastes viviparus* showed the *marinus* haemoglobin pattern. Morphological «intermediates» showed the *marinus* pattern in the Barents Sea while some specimens, which showed the *mentella* hemoglobin patterns, but could not be separated morphologically from the *marinus* type, were recorded in the Icelandic-Faeroe Ridge area. Four specimens showed a haemoglobin pattern which indicated hybridization between individuals with different haemoglobin pattern.

The results indicate that *Sebastes mentella* Travin is a species distinct form *Sebastes marinus* (L), possibly with occasional interbreeding. However, for final conclusion about the species of redfish in the North Atlantic samples have to be collected from the total range of the redfish's distribution.

INTRODUCTION

LUNDBECK (1940) claims that besides the common redfish, *Sebastes marinus* (L), a deep sea type excists in the Bear Island area and on the Iceland-Faeroe Ridge. TRAVIN (1951) described the deep sea redfish from the Bear Island area and the Barents Sea as a new species, *Sebastes mentella* Travin. This species prefers deeper water and somewhat higher temperature than *S. marinus* although they also occur sympatrically. *S. mentella* is characterized by a beak on its lower jaw, possesses a greater eye diameter, grows slower and reaches a smaller total length than *S. marinus*. The colour of *S. mentella* is bright red and of *S. marinus* usually orange-red.

ANDRIIACHEV (1954) and TEMPLEMAN (1959) restricted *Sebastes mentella* to the status of a subspecies, *S. marinus mentella*, because the differences between *marinus* and *mentella* were not clear enough to justify them as two

distinct species. TEMPLEMAN (1959) and others have found that *S. mentella* is not restricted to the Northeast Atlantic, but is common also in the Northwest Atlantic and occurred here in most localities in greater quantities than *S. marinus*.

By meristic, morphometric or morphologic methods clearcut separation of redfishes into *marinus* and *mentella* groups has been difficult (KOTTHAUS 1961, TEMPLEMAN 1959, KELLY, BAKER and CLARKE 1961). A great proportion of the specimens possessed the characteristics of both groups in a varying manner. However, genetical differences between the two groups were suggested by TEMPLEMAN and SANDEMAN (1959) who found great differences between *marinus* and *mentella* types in relative occurrence of caudal melanophores of pre extrusion larvae.

YANULOV (1962 a) found significant differences between the two types in infestation rate of various parasites in parts of the Northwest Atlantic.

By immuno-diffusion techniques, photron-reflectometric measurements and two separate methods of chromatography O'ROURKE (1961) found evidence for biochemical specificity of the two forms to such a degree that they could be considered as two distinct species. Similarly SCHAEFFER (1961) found that the two types differed significantly in content of certain free amino acids and total nitrogen content in muscle tissue.

In a series of papers (ALTUKHOV *et al.* 1968, ALTUKHOV and NEFYODOV 1968, ALTUKHOV, NEFYODOV and PAYUSOVA 1968, NEFYODOV 1969) dealing with the redfish problem, were described differences in muscle termostability and also differences in frequencies of some polymorphic serum proteins chartateristics (haptoglobins, albumins, and β-globulins) between samples of *marinus* and *mentella* types from the waters between Iceland and Greenland, showing tnat the analysed samples were not drawn from one homogenous population.

In the present paper differences in electrophoretic mobility of haemoglobins of the two types of redfish are described, and the results are discussed in relation to their significance on the systematic and the management of the redfish.

MATERIALS AND METHODS

Redfish for blood sampling was caught by bottom trawl. Blood was obtained by a syringe from the heart region, or the fish was cut open and blood collected into small glass tubes. After centrifugation the serum was pipettet off and the cells lysed by adding destilled water.

The haemoglobins were analysed by the agar gel electrophoresis at pH 7.2 describe by SICK (1965). Selected specimens were also analysed by the combined starch and agar gel electrophoresis at pH 9.0 described by MØLLER (1966). The haemoglobins were always analysed within 24 hours, usually

Table 1. Distributions of haemoglobin patterns in redfish from the Barents Sea and Icelandic waters.

Sample no.	Locality	Date of sampling	Depth m	Mentalla-pattern	Marinus-pattern	Others	Sum
1	71°00'N, 20° 00'E	7 November 1970	200	—	30	—	30
2	75°40'N, 16°50'E	10 » »	350	40	—	—	40
3	76°30'N, 13°50'E	12 » »	200	6	24	—	30
4	76°58'N, 12°30'E	12 » »	400	20	—	—	20
5	73°00'N, 33°45'E	17 » »	218	2	18	—	20
6	71°00'N, 34°42'E	19 » »	200	6	19	—	25
7	71°00'N, 29°06'E	19 » »	218	5	55	—	60
8	71°20'N, 26°40'E	20 » »	150	—	100	—	100
	Total, Barents Sea			79	246	—	325
9	64°20'N, 12°36'W	19 August 1971	236	9	27	2	38
10	63°20'N, 25°08'W	13 » »	300	—	158	2	160
11	65°38'N, 26°47'W	16 » »	280	3	156	—	159
	Total, Icelandic waters			12	341	4	357

within 12 hours from sampling. Parts of the material were reanalysed after one or two days. Some haemoglobin specimens were also frozen and later reanalysed at the Institute of Marine Research in Bergen. The haemoglobins were stained by Amidoblack 10 B.

All samples from the Barents Sea were collected and analysed during a cruise by R.V. «G. O. Sars» in November 1970 and the samples from Icelandic waters likewise in August 1971. Fishing localities, depth, date of sampling and number of specimens in each sample are listed in Table 1. Fishing localities are also shown in Fig. 1 and 2.

All redfish specimen were separated morphologically into *Sebastes viviparus* [backward directed anterior preopercular spine (Andriiashev 1954)], *mentella* type, *marinus* type and intermediates [according to the description by Travin (1951)], and separation by morphology was compared to the results from the haemoglobin analyses. Total length, usually also sex, were recorded for the fishes of which blood was collected.

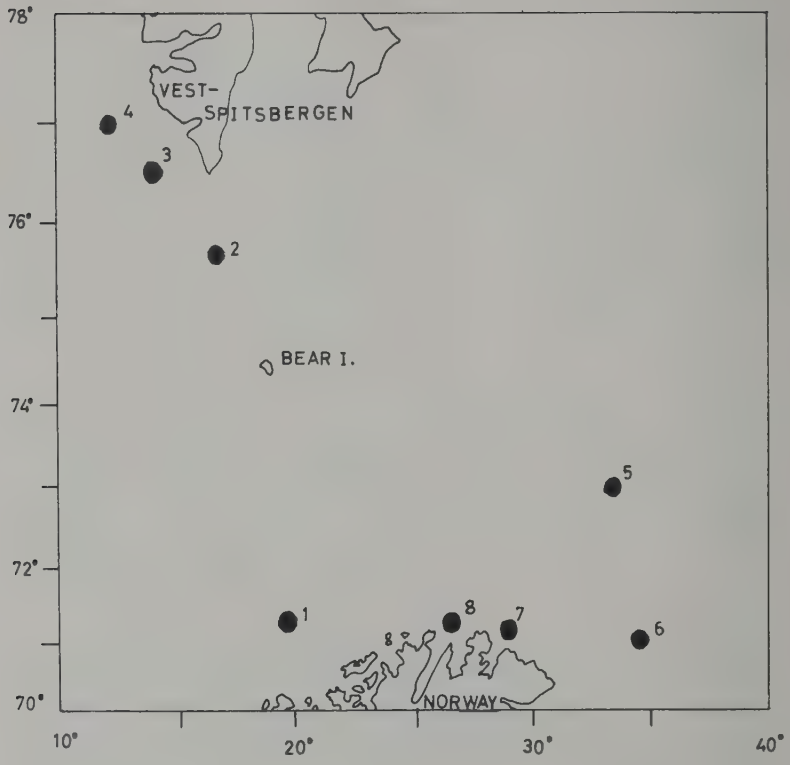

Fig. 1. Sampling localities of redfish in the Barents Sea.

RESULTS

HAEMOGLOBIN TYPES OF REDFISH FROM THE BARENTS SEA

Among the samples from the Barents Sea were found two main haemoglobin patterns (Fig. 3). The first pattern occurred in specimens which according to TRAVIN (1951) were of the *mentella* type. In agar gel at pH 7.2 this pattern showed a strong, but rather diffuse anodic moving component, and one weak component stayed near the origin. By combined starch and agar gel electrophoresis at pH 9.0 the strong component showed high anodic mobility. Two weak components also showed anodic mobility while one very weak component moved slightly towards the cathode. This pattern was tentatively called the *mentella* pattern.

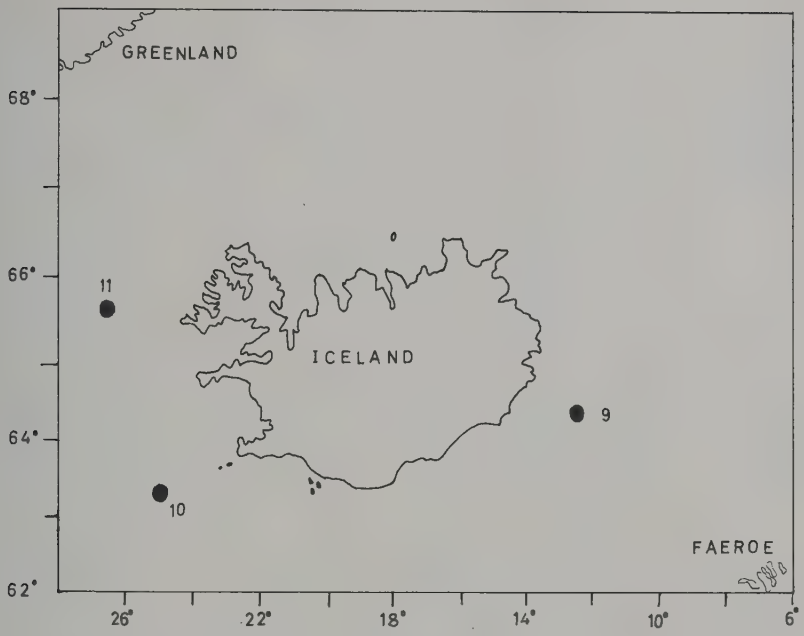

Fig. 2. Sampling localities of redfish in Icelandic waters.

The second pattern was found in specimens morphologically determined to be of the *marinus* type and consequently was called the *marinus* pattern. At pH 7.2 all components moved towards the cathode. Two weak components showed the highest mobility, and one strong component moved only slowly.

Individual variations were indicated in strength and occurrence of the two weak components, but this variation was not clear enough to form the basis of clearcut classification of the specimens. At pH 9.0 the strong component of the *marinus* pattern moved slower towards the anode than the strong component of the *mentella* pattern. Also in the *marinus* pattern was seen two weak components, one with intermediate anodic mobility and one with slight cathodic mobility.

One *Sebastes viviparus* from the Barents Sea (sample 1) showed the same haemoglobin patterns as individuals of the *marinus* type. Some specimens possessed morphological characteristics both of *marinus* and *mentella* types. This was especially evident at one locality on the Norwegian coast (sample 8) where the greater part of the specimens were recorded as such «intermediates» (SMESTAD, unpublished). However, with no exception all these specimens showed the *marinus* haemoglobin pattern.

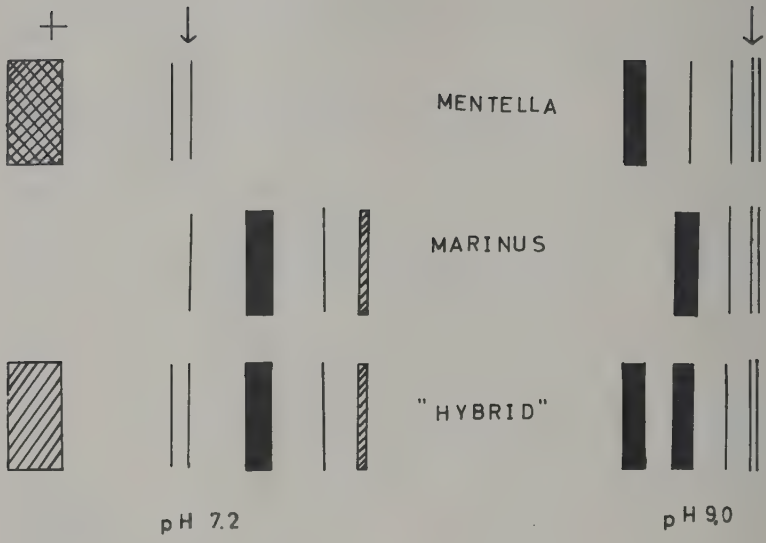

Fig. 3. Outline of haemoglobin patterns in redfish obtained by gel electrophoresis. Filled in bars: Strong bands. Hatched bars: Moderately strong bands. Single lines. Faint bands. Arrow indicate the points of application.

The analysed specimens varied in length from about 15 to 40 cm, and both haemoglobin patterns were observed among the smaller as well as among the greater specimens. Consequently, no indications of ontogenetic variation in haemoglobin patterns were found in redfish.

The haemoglobin pattern could be recognized also after freezing and thawing of the hemolysate, but the clearest patterns were obtained with fresh material. No *post mortem* variation, except that the total patterns became diffuse, could be observed after proponged storage in the refrigerator.

The distribution of the two different patterns in the samples from the Barents Sea are shown in Table 1 (sample 1–8). The *mentella* pattern was found most frequently in the area between Bear Island and Spitsbergen and were rare in the eastern parts of the Barents Sea and near the Norwegian coast. Both were found together in the same trawl haul, but *mentella* occurred more frequently in deeper water. This is in accordance with the general appearence of the *mentella* type of redfish for instance from the description of Travin (1951).

Similar *mentella* and *marinus* haemoglobin patterns occurred among redfish samples from Icelandic waters as in the samples from the Barents Sea. In some specimens a modified *marinus* pattern occurred. This pattern showed an extra component which in agar gel at pH 7.2 moved slightly towards the anode and in combined starch and agar gel electrophoresis at pH 9.0 moved towards the anode with a mobility greater than the common strong component of the *mentella* pattern.

Totally 88 specimens of sample 10 and 19 specimens of sample 11, which were supposed to be *S. viviparus* from their backward directed preopercular spines, showed one of the two *marinus* patterns.

Few *mentella* patterns were found in Icelandic waters. West of northern Iceland (sample 11) were found three specimens out of 159 which showed the *mentella* pattern, and the fishes which possessed these patterns, were easily distinguished morphologically. West of Reykjanes (sample 10) were found no *mentella* patterns, and on Iceland-Faeroe Ridge (sample 9) were found 9 *mentella* patterns out of totally 38 specimens. In this sample all but one of the smaller fishes (9–13 cm) showed the *mentella* pattern, and also three fishes about 40 cm in length showed this pattern. However, in contrast to all other samples, morphological differentiation of the fishes showing the different haemoglobin types was nearly impossible, even for the greater specimens.

Four specimens, two in each of sample 9 and 10, showed a haemoglobin pattern with both the component of *mentella* and *marinus* pattern (Fig. 3). Morphologically these four specimens could not be distinguished from the *marinus* type, but because the pattern indicates hybridization between individuals with different haemoglobin types, this pattern tentatively was called the «hybrid» pattern. The fishes which showed this pattern ranged in length from 36 til 45 cm.

DISCUSSION

The compositions by amino acids of the proteins polypeptide chains and consequently the electrophoretic mobility of the proteins are controlled by genetic factors (Manwell and Baker 1970). The electrophoretic patterns of fish haemoglobins usually are species specific, illustrated by among others Tsuyuki *et al.* (1968) who described species specific electrophoretic patterns of haemoglobins of 28 species Pacific Ocean Scorpaenidae. Intraspecific variations of haemoglobin patterns, controlled by codominant alleles, have been described for several species (see de Ligny 1969 for references). In other species, for example salmon (Koch, Bergstrøm and Evans 1966) and herring (Wilkins and Iles 1966), intraspecific variations have been obser-

ved to be connected with ontogeny. Also variations due to changes in haemoglobin components after prolonged storage of samples have been described for several species, but these variations usually are found in the minor haemoglobin components (Sick 1965, Møller and Nævdal 1969, Tsuyuki *et al.* 1968, Nævdal 1968).

Neither ontogenetic cariation nor *post mortem* changes can account for the observed patterns of redfish haemoglobins because the two common patterns were observed in fishes ranging from less than 10 cm to more than 40 cm in length, all specimens were given the same treatment, and all were analysed within 24 hours from sampling. Control specimens did not show any major change in patterns even after two or three days in refrigerator or after freezing and thawing.

Segregation of two codominant alleles within one species could produce three patterns like the main patterns observed (the *mentella* and *marinus* patterns as homozygotes and the «hybrid» pattern as heterozygote). However, according to the Hardy-Weinberg law the hypothetical heterozygote (here the «hybrid» pattern) should then be expected to occur much more frequently than observed. It therefore seems unlikely that haemoglobin variation within one species can account for these patterns, but the modified *marinus* pattern in redfish from Icelandic waters may be normal intraspecific variation, probably genetically controlled.

However, the two common patterns may be explained by assuming that the *mentella* and *marinus* types of redfish really belong to different species, each with their own haemoglobin pattern. The «hybrid» pattern may be due to occasional hybridization between individuals of the two species. The good agreement, except in sample 9, between the results from the analyses of haemoglobins and morphological differenciation strongly support the theory of two species. Four hybrids out of more than 650 individuals do not show that the two types are conspecific because hybridization between related species is not uncommon among fishes. According to a second theory the «hybrid» pattern may represent an intraspecific variant of the *marinus* type. This theory is supported by the fact that the four specimens with the «hybrid» haemoglobin pattern could not be distinguished morphologically from the *marinus* type.

Although the *mentella* and *marinus* type of redfish seem to represent different species with only occasional interbreeding in the Barents Sea and Icelandic waters, the possibility still excist that the two types may be connected through intermediate populations in other areas. A definite conclusion about the species of redfish in the North Atlantic can therefore not be drawn until samples have been collected from the total geographic range of the redfish. However, the *marinus* and *mentella* types of redfish surely represent different *gene pools* with a minimum exchange of genetic material, and they therefore should be treated as separate units in management of the North-

east Atlantic fisheries. In addition, both the *mentella* and the *marinus* types may be composed of smaller units (populations, stock units) as claimed by SINDERMANN (1961) and YANULOV (1962 a, b) and others in their studies of parasites and meristic characteristics.

The fact that *Sebastes viviparus* showed the *marinus* haemoglobin pattern has no effect upon this conclusion. *Sebastes viviparus* doubtless is a true species (ANDRIIASHEV 1954, TROUT 1961), and two related species may have similar haemoglobin structure while others differ widely.

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ASPECTS OF THE LIFE HISTORY OF THE LOCAL HERRING STOCK IN LINDÅSPOLLENE, WESTERN NORWAY

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ABSTRACT

LIE, U., DAHL, O. and ØSTVEDT, O. J. 1978 Aspects of the life history of the local herring stock in Lindåspollene, western Norway. *Fisk.Dir. Skr. Ser. Hav.Unders.*, *16*: 369–404.

Gill net and purse seine samples were obtained during 1970–1974 for studies of the biology of the local herring stock in a landlocked fjord, Lindåspollene, in western Norway. The herring stock revealed a distinct migration pattern within the system, with a well defined spawning, feeding and overwintering area. The mean number of vertebrae was 56.70. The age, as determined from scale readings, reached 15 years, but only about 2% exceeded 10 years of age. The growth of the Lindås herring was slower than that of the Atlanto-Scandian or North Sea herring stocks, reaching $L\infty = 30.49$ cm. The raw weight of the largest individuals was about 250 g. The condition factor reached its maximum in August–October and minimum in May. The mean weight loss during spawning was about 20% of the total weight. The herring spawned in late March, usually in a small fjord arm at depths ranging from 0 to 4 m. Studies of the fecundity showed large variability in number of eggs within length groups. The strength of the year classes and the growth rate of the Lindås herring is discussed in relation to biotic and abiotic conditions of the environment.

INTRODUCTION

Along the Norwegian coast there are a number of small fjords and semi enclosed bays («poll» in Norwegian) in which there are small, more or less self contained herring populations. These local herring stocks can usually be readily distinguished from the oceanic herring by the growth characteristics, and some of the populations have been subjected to scientific studies previously (AASEN 1952, 1953, RASMUSSEN 1941, 1958).

The symposium arranged by the International Council for the Exploration of the Sea (ICES) on «Herring population studies» in Copenhagen, 1961, recommended intensive studies of small, self contained populations in order to throw light upon problems such as reproduction, larval ecology, growth and tagging techniques, which only with extreme difficulties could be studied on oceanic herring populations (ANON. 1963).

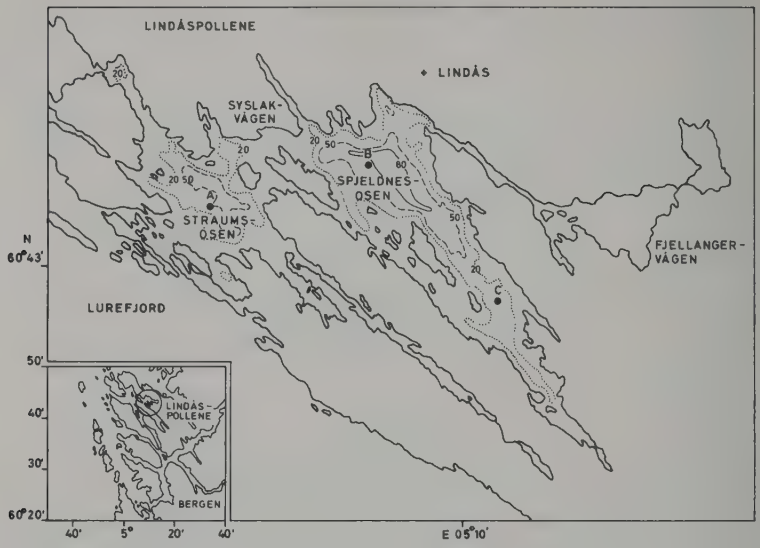

Fig. 1. Depth contour lines and hydrographical stations in Lindåspollene.

Following this recommendation, studies on a number of local herring populations in western Norway were carried out during 1962–1963 (ANON. 1969). The local stocks were as a rule rather strongly mixed with coastal herring which migrated in and out of the «polls» but the herring in Lindåspollene (Fig. 1) appeared to be less influenced by «strange» herring than the other stocks investigated. The Institute of Marine Research, Directorate of Fisheries, therfore decided to undertake intensive studies of the local herring stock in Lindåspollene. The primary emphasis should be on the description of the natural history and the population dynamics of the herring which would be a basis for studies of the relationships between stock and exploitation.

It was realized that the population parameters of the herring stock are intimately related to biotic and abiotic factors of the environment, and therefore it was decided to carry out studies of the entire ecosystem in Lindåspollene simultaneously. The Institute of Marine Biology, University of Bergen, would be responsible for the investigation on the Lindåspollene ecosystem. An outline of the research topics and the objectives of the co-operative studies between the Institute of Marine Research and the Institute of Marine Biology has been given by DAHL, ØSTVEDT and LIE (1973).

The present paper reports on the studies of the herring in Lindåspollen during the period 1970–1974, with particular emphasis on aspects of the

Table 1. Herring samples from Lindåspollene (1970–1974).

No.	Date	Number of fish	Gear	No.	Date	Number of fish	Gear
1a	23 August-70	84	Purse seine	26	4 October-72	23	Gill nets
1b	4 October-70	16	Gill nets	27	12 October-72	139	Purse seine
2	11 Nov.-70	16	»	28	9 Nov.-72	286	Gill nets
3	28 Nov.-70	100	»	29	7 Decemb.-72	4	»
4	27 January-71	76	»	30	10 January-73	24	»
5	26 Febr.-71	24	»	31	1 Febr.-73	21	»
6	18 March-71	37	»	32	23 March-73	7	»
7	28 March-71	119	»	33	28 March-73	27	»
8	22 April-71	80	»	34	29 March-73	31	»
9	5 May-71	7	»	35	11 April-73	25	»
10	10 May-71	90	»	36	25 July-73	15	»
11	8 June-71	8	»	37	15 August-73	8	»
12	10 June-71	100	»	38	23 August-73	40	»
13	29 July-71	26	»	39	12 Sept.-73	100	Purse seine
14	17 August-71	150	Purse seine	40	12 Sept.-73	124	»
15	8 Sept.-71	100	»	41	25 October-73	23	Gill nets
16	20 Sept.-71	70	Gill nets	42	16 January-74	63	»
17	19 October-71	19	»	43	20 Febr.-74	30	»
18	22 Nov.-71	150	»	44	14 March-74	83	»
19	26 January-72	275	»	45	21 March-74	147	»
20	9 March-72	57	»	46	28 March-74	8	»
21	22 March-72	37	»	47	2 April-74	100	»
22	26 April-72	14	»	48	27 July-74	9	»
23	25 May-72	7	»	49	21 August-74	36	»
24	25 May-72	15	»	50	5 Sept.-74	50	Purse seine
25	31 August-72	75	»				

life history and population dynamics of the herring. The material, which is the basis for the study, did not lend itself to estimates of stock abundance, and important topics such as recruitment, mortality, production and yield have therefore been ommitted in this report.

MATERIAL AND METHODS

The present paper is based on 44 gill net samples containing 2428 herring collected during the period October 1970–September 1974 and five purse seine samples collected during the period August–October of 1970, 1971, 1972, 1973 and 1974 (Table 1).

The gill nets (52 mm mesh size) were set on localities in Lindåspollene which are traditionally good fishing grounds (Fig. 2), and the plan was to obtain one sample per month. However, during the summer months the catches were often negative, and in February and December 1973 fishing was prevented by ice. On some occasions, particularly during the spawning

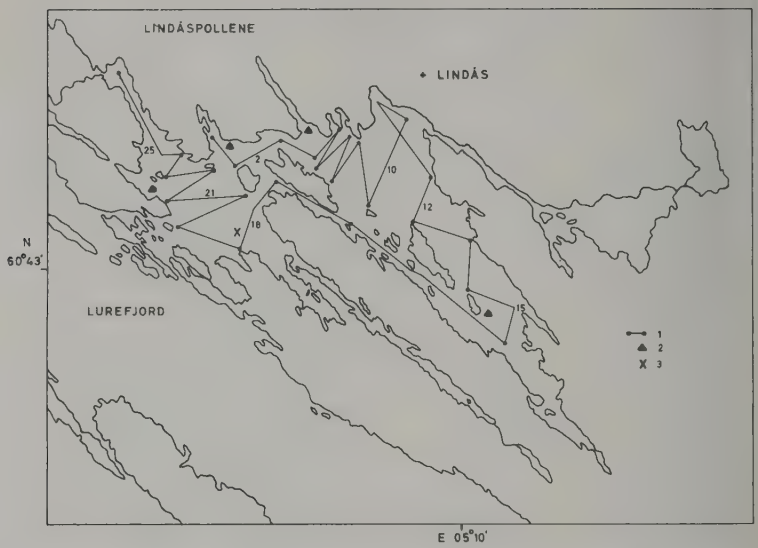

Fig. 2. Echo survey course tracks (1) gill net (2) and purse seine (3) sampling localities.

season, more than one sample was obtained in the same calender month. Data were then pooled to give monthly samples.

The purse seine catches were obtained with seines designed for commercial sprat fishing, and the sampling took place at night using artificial light. The samples contained several age groups of herring, with a preponderance of immature year classes. The purse seine catches were always made in the southern part of Straumsosen (Fig. 2).

The migrations of the herring within the Lindåspollene were determined from observations of the horizontal and vertical distribution of the herring during the investigated period. The observations were made on acoustic surveys which since March 1972 were made along fixed cruise tracks (Fig. 2). During the period August 1970–December 1973 the surveys were made with a SIMRAD EM2F (38kHz) echosounder and during 1974 with a SIMRAD EY (80kHz) echosounder.

The vertabrae were counted on 846 individuals from the gill net samples.

Length of 2421 individuals was measured from the tip of the snout to the longest caudal fin ray, with the lobes of the tail in the mid line (ANON. 1963). The lengths were measured to the nearest ½ cm below and subsequently grouped to the nearest cm below. True mean lengths have therefore been obtained by adding 0.5 cm to the calculated mean lengths.

Wet weights of 2233 herring were determined to the nearest 5 g, and grouped into 10 g intervals.

The nutritional state of the herring was expressed by the condition factor (FULTON 1911):

condition factor (K) = weight (W)/length $(L)^3$

and by the relative amount of intestinal fat classified according to AASEN (1952) into:

class 0: no fat,
class I: traces of fat,
class II: moderate fat,
class III: much fat.

The age of 2067 individuals was determined by reading the winter rings on the scales. Back calculations of lengths from measurements on the scales were performed on all the herring caught on the gill nets during 1971, using the formula of LEA (1910) and ANON. (1963)

$$l_n = \frac{s_n}{s} L$$

where s_n = radius of scale annulus at age n, s = scale radius, L = length of fish at sampling. Since length at sampling was measured to the nearest $^1/_2$ cm below, 0.25 cm has been added to obtain true mean lengths.

The maturity stages of the herring were determined by the method of JOHANSEN (1919) as modified bye the ICES Working Group on Methods used in the North Sea Herring Investigations (ANON. 1963):

STAGE

I Virgin herring. Gonads very small, threadlike, 2–3 mm broad. Ovaries wine red. Testes whitish or grey brown.

II Virgin herring with small sexual organs. The height of ovaries and testes about 3–8 mm. Eggs not visible to naked eye but can be seen with magnifying glass. Ovaries a bright red colour; testes a reddish grey colour.

III Gonads occupies about half of the ventral cavity. Breadth of sexual organs between 1 and 2 cm. Eggs small but can be distinguished with naked eye. Ovaries orange; testes reddish grey or greyish.

IV Gonads almost as long as body cavity. Eggs larger, varying in size, opaque. Ovaries orange or pale yellow, testes whitish.

V Gonads fill body cavity. Eggs large, round; some transparent.Ovaries yellowish; testes milkwhite. Eggs and sperm do not flow, but sperm can be extruded by pressure.

VI Ripe gonads. Eggs transparent; testes white; eggs and sperm flow freely.

VII Spent herring. Gonads baggy and bloodshot. Ovaries empty or containing only a few residual eggs. Testes may contain remains of sperm.

VIII Recovering spents. Ovaries and testes firm and larger than virgin herring in Stage II. Eggs not visible to naked eye. Walls of gonads striated; blood vessels prominent. Gonads wine red colour. (This stage passes into Stage III).

The number of eggs per unit weight of the gonads was determined by counting parts of gonads from 73 herring under a dissecting microscope. The gonads were preserved in Gilson's fluid and treated according to BAXTER (1959) before counting. Total number of eggs per gonad was determined by multiplication with total gonad weight. The fecundity of an additional 45 herring was determined by complete counting of eggs in the ovaries by an automatic particle counter (BERGE and PETTERSEN 1974).

RESULTS

MIGRATIONS

In a preliminary report on the acoustic surveys during 1971–1972 and the first three months of 1973, ØSTVEDT, DAHL and LIE (1973) discussed the apparent migration pattern of the herring in Lindåspollene. The major conclusions were:

a) the herring spawned in Syslakvågen in late March,
b) after spawning the herring moved into Straumsosen and remained there during the summer,
c) in September–October the herring moved into Spjeldnesosen and scattered,
d) in November–December the herring concentrated in the northern part of Spjeldnesosen and remained there until spawning in March.

This migration pattern was largely confirmed by the investigations during 1973–1974, but there were also some major discrepancies between the two periods of investigation. Thus, there was no spawning migration into Syslakvågen in 1973, and no other spawning area was located. In 1974 the herring had a normal spawning migration into Syslakvågen.

The migration pattern after spawning was also somewhat different in 1973–1974 because a part of the stock moved south into Spjeldnesosen and remained there during the summer. However, the major part of the stock moved into Straumsosen as during 1971–1972.

On the basis of all the acoustic surveys performed during 1971–1974 a migration pattern, as demonstrated in Fig. 3A, B og C, is suggested. The pattern during September–March is repeated each year, but the distribution during the rest of the year is less clear. Thus, the migration to the spawning grounds must be further studied and also the distribution during May–August.

ØSTVEDT *et al.* (1973) discussed the vertical distribution of the herring and concluded that the herring during the winter was distributed at about 50–60 m depth. The distribution during the summer was higher up in the sea. They also demonstrated vertical diurnal migrations, with a distribution near the surface at night.

The acoustic surveys during 1973–1974 were carried out during daytime, and the herring was as a rule distributed at intermediate depths (Fig. 4).

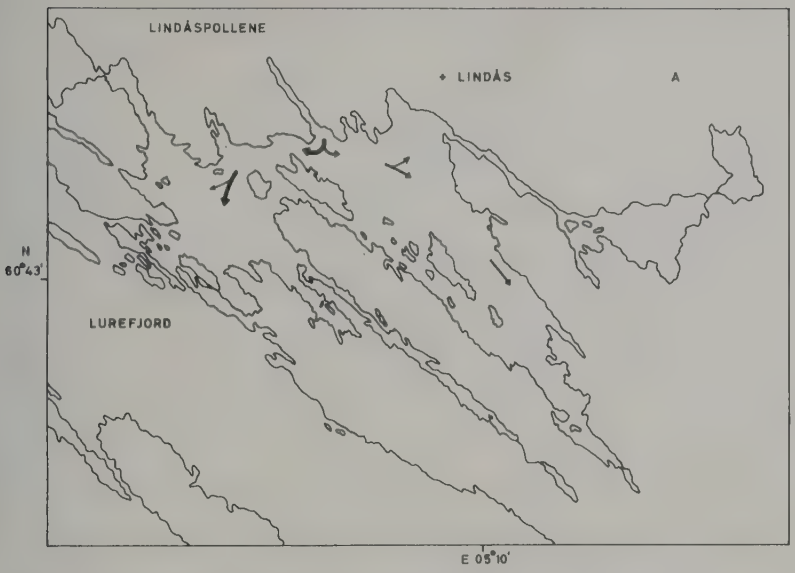

Fig. 3A. Migration pattern of the Lindås Herring during April–August.

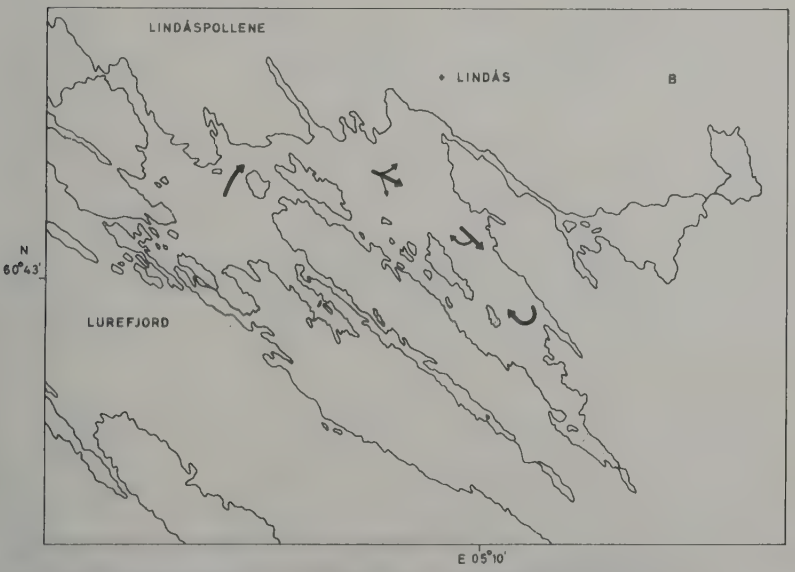

Fig. 3B. Migration pattern of the Lindås herring during September–October.

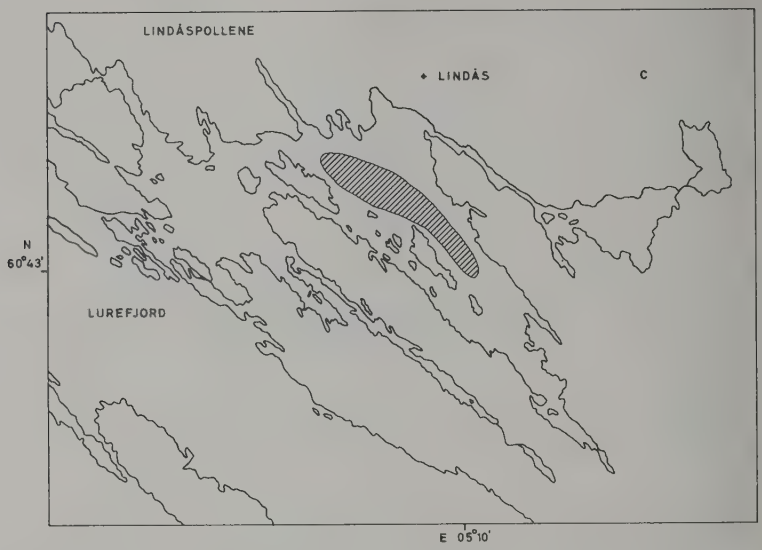

Fig. 3C. Migration pattern of the Lindås herring during November–March.

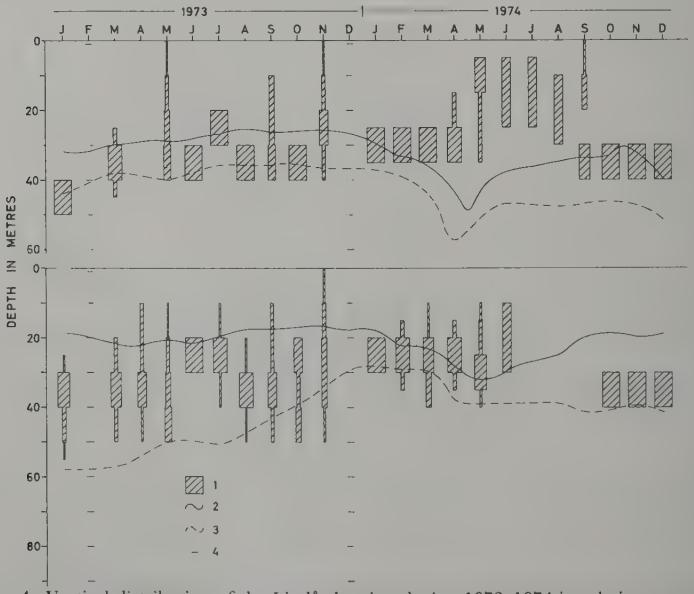

Fig. 4. Vertical distribution of the Lindås herring during 1973–1974 in relation to oxygen concentration of the water masses. 1) Herring concentration, 2) 4,0 ml O_2/l [3]) *1,0 ml* O_2/l, 4) no observation.

Table 2. Frequency distribution of number of vertebrae of the herring in Lindåspollene during 1970–1973.

Data	Number of vertebrae						Mean	n	S^2	± C.I.
	54	55	56	57	58	59				
1970										
October	—	—	7	6	2		56.67	15	0.524	0.3738
November ...	1	1	41	56	16	1	56.76	116	0.837	0.1698
1971										
January	—	1	21	45	4	—	56.73	71	0.763	0.2073
February	—	—	7	13	4	—	56.88	24	0.535	0.2986
March	—	4	41	42	10	1	56.62	98	0.527	0.1467
April	1	2	28	33	10	—	56.66	74	0.636	0.1854
May	2	5	20	52	6	—	56.65	85	0.636	0.1730
August	—	—	10	35	5	—	56.90	50	0.296	0.1539
September ...	—	4	20	28	18	—	56.86	70	0.762	0.2087
November ...	—	7	33	46	11	—	56.63	97	0.611	0.1587
1972										
January	3	7	27	52	7	—	56.55	96	0.734	0.1748
1973										
September ...	—	2	20	22	6	—	56.64	50	0.561	0.2118
Total	7	33	275	430	99	2	56.70	846	0.589	0.0528

There was a tendency for the herring to be concentrated nearer the surface during the summer. It should be noticed that the data in the figure are percentages, and therefore the figure gives no information about the strength of the recordings between months. Thus, the data for Straumsosen during September–April and for Spjeldnesosen during May–August are based on very few and scattered recordings.

Fig. 4 shows that the majority of the recordings were made in the water layer limited by the isolines for 1 ml 0_2 per litre and 4 ml 0_2 per litre, and particularly during the winter the herring seems to remain in water masses characterized by very low oxygen tension. This is peculiar for a pelagic fish, and Kamshilov and Gerasimov (1960) demonstrated that young Murman herring kept in aquaria died in oxygen concentrations below 2 ml per litre.

IDENTIFICATION OF THE POPULATION

The preliminary investigations in Lindåspollene during 1962–1964 showed the presence of two distinct components in the herring stock: a) a slow growing component which constitute the major part of the stock, and b) a fast growing component which was considerably less important (Anon. 1964). The latter component was referred to as the «strange» herring, in accordance with Aasen (1952).

Table 3. Analyses of variance on vertebrae counts.

Source of variation	df	SS	MS	F
Among months	11	19.30	1.75	2.97 (P 0.01)
Within months	834	489.50	0.59	
Total	845	508.80		

Vertebral counts as a means of distinguishing between populations or «races» of herring from northern European waters has been used by a number of authors (viz. Runnstrøm 1941, Aasen 1952, Cushing 1958 and Zijlstra 1958). In order to investigate the possible relationships between the Lindås herring and neighbouring herring stocks, vertebrae were counted in 846 individuals collected during the period October 1970– September 1973.

The monthly mean number of vertebrae in the herring from the gill net samples ranged from 56.55 to 56.90, with an overall mean of 56.70 (Table 2). An analysis of variance (Table 3) showed that there was a significant added variance component among months, but this component did not amount to more than 0,95% of the total variance, and there was no distinct seasonal or annual trend in the monthly mean number of vertebrae.

It is not unexpected that herring samples collected during a timespan of about three years would reveal differences in the mean number of vertebrae. In the first part of the investigated period the samples were strongly dominated by the 1966 year class, but from about August 1972 the 1969 year class became increasingly more important. It is conceivable that variability in the sea temperatures on the spawning grounds could cause differences in the number of vertebrae of various year classes. An inverse relationship between number of vertebra and the sea temperatures on the spawning grounds has been demonstrated by a number of authors, and considerable fluctuations in the temperatures on the shallow spawning ground in Syslakvågen must be expected.

During 1962–1964 the «strange» herring had a mean verebral count of 57.0 to 57.2 whereas the slow groving component of the Lindås herring had a mean vertebral count of from 56.4 to 56.6 (Anon. 1964). The «strange» herring during the period 1970–1973 had a mean vertebral count of 56.65 and could therefore not be distinguished significantly from the slow growing component. Thus, there seems to have been a distinct change in the number of vertebrae in the «strange» herring from 1962–1964 to 1970–1973. In 1962–1964 the number of vertebrae in the «strange» herring could not be significantly distinguished from the Atlanto Scandian herring stock (Anon 1964), and during 1970–1973 the number of vertebrae did not differ from that of the North Sea spring spawning stock (Table 4). Hence,

Table 4. Mean vertebrae numbers of the year class 1969 from different groups of spring spawning herring.

Race	V. S. Mean	Number	S^2	± C.I.
Lindås herring	56.64	462	0.591	0.0715
North S. herring	56.84	107	0.380	0.1192
Atlanto Scandian herring ...	57.02	631	0.371	0.0485

the hypothesis cannot be rejected that the «strange» herring in Lindåspollene during 1962–1964 represented specimens from the Atlanto Scandian stock, and during 1970–1973 from the North Sea spring spawning stock. It is noteworthy that the change in the apparent origin of the «strange» herring component coincided with the drastic reduction of the Atlanto Scandian herring stock (Devold 1968).

The mean number of vertebrae in the slow growing component of the 1969 year class Lindås herring was quite similar to the mean number of vertebrae of the North Sea herring of the same year class (Table 4). The difference to the Atlanto Scandian stock of the same year class was more pronounced and significant beyond the 99% level of probability.

AGE

The age of the herring in Lindåspollene can easily be determined by scale readings because the winter growth rings are always well defined (Fig. 5), similar to the northern growth type of the Atlanto Scandian herring stock (Lea 1929). The age at first spawning can also often be ascertained because the growth ring during the preceding summer is distinctly reduced.

The age was determined by scale readings from 2067 individuals collected with gill nets during the period October 1970–September 1974 (Table 5). Some two year old herring were caught by the gill nets, but the population does not seem to become fully vulnerable until the fourth year.

The herring in the gill net samples ranged in age from 2 to 15 years, but only about 2% were older than 10 years. Thus, the Lindås herring is relatively short lived compared to the Atlanto Scandian herring stock where specimens reaching 24–25 years of age were frequently caught in years of high stock abundance and low fishing mortality (Devold and Dahl 1964).

The 1966 year class was strong during 1971, but from the second quarter of 1972 the 1969 year class became increasingly dominant (Table 5). Subsequently, there was a reduction in the relative strength of the 1966 year class. On the basis of the relative strengths of the year classes alone, it cannot

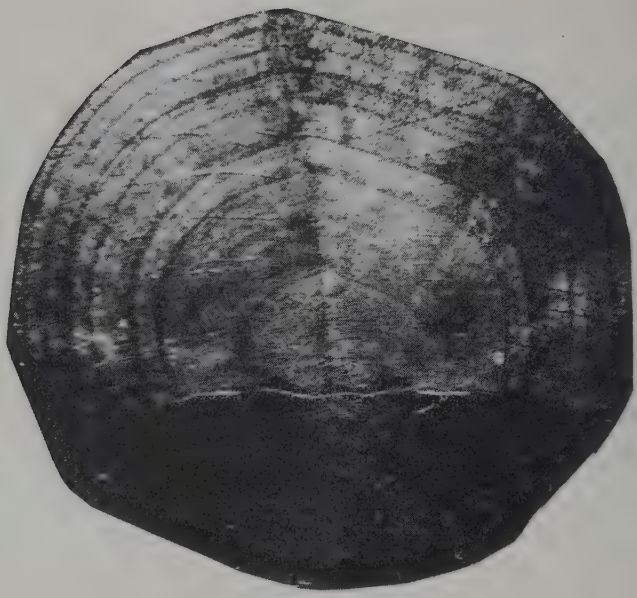

Fig. 5. Growth rings in the scale of a Lindås herring.

be determined whether the decrease in the percentages of the 1966 year class is a result of the emergence of a very strong 1969 year class, or if there was a concurrent increase in the mortality of the 1966 year class.

Table 6 shows that the 1964, 1965, 1967 and the 1968 year classes were weak whereas there is some indication that the 1962 and the 1963 year classes had been relatively strong. The preliminary investigations in Lindåspollene during 1962–1964 demonstrated that the 1959 year class was strongly dominant during that period (DAHL *et al* 1973).

LENGTH AND GROWTH

The length of the herring from the gill net samples collected during the period October 1970–September 1974 ranged from 21 to 35 cm, but about 90% of the individuals measured from 25 to 30 cm (Table 7). The majority of the individuals larger than 31 cm belonged to the «strange» herring component. The monthly mean lengths were not significantly different during 1970–1971 when the 1966 year class dominated in the samples, averaging 27.34 cm. However, there was a distinct decrease in the mean length from August 1972 when the 1969 year class became more predominant. Thus, the average of the monthly mean lengths during 1973 were only 25.57 cm.

Table 5. Seasonal composition (%) in the age structure of the Lindås herring, 1970–1974 (gill nets).

Date	Age in years														n
	2	3	4	5	6	7	8	9	10	11	12	13	14	15	
1970															
October–December	0.8	2.4	75.9	7.3	0.8	4.8	5.6	0.8	0.3	0	0.8	0	0	0	124
1971															
January–March	2.2	3.9	8.7	53.4	9.1	1.3	6.5	7.8	1.7	0.4	0	0	0	0	230
April–June	0.4	5.6	6.4	76.4	6.7	0	1.9	2.2	0	0	0	0.4	0	0	267
July–September	2.2	3.3	7.8	61.1	8.9	6.7	4.4	2.2	0	2.2	0	0	0	0	90
October–December	10.1	10.7	3.8	43.4	6.9	3.8	3.8	13.2	3.1	0	0.6	0	0	0.6	159
1972															
January–March	0	5.0	4.7	1.8	48.9	10.9	2.5	4.0	11.2	3.3	1.8	1.1	0.4	0.4	276
April–June	10.3	17.0	13.8	10.3	24.1	3.4	3.4	3.4	6.8	6.8	0	0	0	0	29
July–September	8.3	44.4	5.5	5.5	30.6	0	0	2.3	1.4	1.4	0	0	0	0	72
October–December	3.2	32.5	4.5	2.5	42.7	0.6	1.3	5.7	3.3	1.3	1.9	0	0	0	157
1973															
January–March	2.8	12.1	54.3	6.5	2.8	15.0	0	2.3	2.3	0	0.9	0	0	0	107
April–June	0	8.0	88.0	0	0	4.0	0	0	0	0	0	0	0	0	25
July–September	10.4	6.2	81.3	0	0	2.1	0	0	0	0	0	0	0	0	48
October–December	5.0	10.0	75.0	0	0	5.0	5.0	0	0	0	0	0	0	0	20
1974															
January–March	7.6	10.2	10.2	64.0	3.4	0	3.4	0.6	0.3	0	0.3	0	0	0	325
April–June	0	0	3.1	75.0	9.5	2.1	8.3	0	1.0	1.0	0	0	0	0	96
July–September	33.3	40.5	4.8	21.4	0	0	0	0	0	0	0	0	0	0	42

Table 6. Annual age composition (%) of the Lindås herring samples in the years 1970–1974 (gill nets).

Years	Age										n
	2	3	4	5	6	7	8	9	10	<10	
1970	0.8	2.4	75.9	7.3	0.8	4.8	5.6	0.8	0.8	0.8	124
1971	3.2	5.9	6.7	62.1	7.8	2.0	4.0	6.3	1.2	0.8	746
1972	2.6	19.6	5.5	3.1	45.8	6.5	2.2	4.3	7.5	5.9	534
1973	4.5	8.5	67.0	3.5	1.5	10.5	0.5	1.5	1.5	1.0	200
1974	5.9	7.8	8.6	66.4	4.8	0.5	4.5	0.5	0.5	0.5	463

Table 7 indicates that the herring in Lindåspollene did not b ecome fully vulnerable to the gill nets before they had reached a length of about 24 cm.

The length distribution of the herring caught in the purse seine in the autumn of each of the years 1970–1974 indicates the relative strengths of the year classes that were not vulnerable to the gill nets at the time of sampling (Table 8). The samples from 1970 and 1971 were strongly dominated by the 1969 year class, and the absence of the 1970 and 1971 year classes as 0- or 1-group indicates that the latter year classes were weak. The 1972 year class, however, was very abundant in the 1972 sample as 0-group, in the 1973 sample as 1-group and in the 1974 sample as II-group which indicates that the 1972 year class is relatively strong.

The length-at-age was determined by back calculations from scale readings for 626 herring caught during 1971. Considerable and statistically significant differences among the year classes regarding growth during the first four years of life were clearly discernable (Table 9). The 1965, 1967 and 1968 year classes had significantly higher l_1, l_2, and l_3 than the year classes 1962, 1963 and 1966. The l_1 and l_2 for the 1969 year class indicate that it belongs to the latter group. In the comparison of lengths-at-age for different year classes it should be kept in mind that the results will be biased by presence of Lee's phenomenon (Lee 1920), and this would particularly apply to the 1962 and 1963 year classes in the present study. However, since the lengths-at-age are determined from the individuals caught in 1971 only, the importance of the Lee's phenomenon cannot be estimated.

It is an interesting fact that the year classes which were classified as relatively strong on the basis of the age frequencies (Table 6) were precisely the year classes characterized by low l_1 and l_2. This indicates that the growth rates during the first years of life may be density dependent. It seems also that slow growth during the first year of life is not compensated by more rapid growth during the following 2–3 years.

The length-at-age as determined for the entire 1971 material is shown in

Table 7. Length frequency distributions, true mean lengths (L), and 95% confidence intervals (C.I.) of the means, of herring from gill-net samples in Lindåspollene, 1970–1974.

	Length, cm										n	Mean L(cm)	± C.I.
	<24	24	25	26	27	28	29	30	31	>31			
1970													
October ...			2	4	8	1		1			16	27.25	0.59
November .		1	3	28	36	17	12	13	5	1	116	28.09	0.28
1971													
January ...			1	8	34	10	11	8	4		76	28.32	0.33
February ..		2	1	6	6	3	2	1		1	22	27.55	0.79
March.....	1	1	12	25	48	26	23	9	6	5	156	28.13	0.30
April		1	9	20	31	14	3	2			80	27.31	0.26
May		1		12	50	23	5	3	2		96	27.86	0.22
June			3	18	49	24	8	4	2		108	27.83	0.27
July	1	2	1	5	9	7			1		26	27.27	0.63
September .			4	8	19	17	10	9	3		70	28.36	0.36
October ...	1	1	1	1	3	2	2	4	4		19	28.76	1.13
November .	1	13	8	20	24	32	23	25	4		150	28.10	0.31
1972													
January ...			12	16	71	74	60	36	5	1	275	28.54	0.16
March		2	1	8	23	29	12	12	6	1	94	28.60	0.33
April	1	3		2		2	3	1	1	1	14	27.86	1.67
May				1	5	1	9	5	1		22	29.18	0.56
August	1	12	12	11	13	16	4	3	3		75	27.10	0.45
October ...	2	7	5	4	2	1	1	1			23	25.89	0.76
November .	2	6	26	32	25	68	66	43	14	4	286	28.53	0.22
1973													
January ...	1	4	5	2	3	2	6	1			24	27.04	0.87
February ..	5	2	5	3	2	3	1				21	25.88	0.80
March.....		8	23	8	8	4	6	6	2		65	26.95	0.46
April	1	14	4	4		1	1				25	25.30	0.55
July	9	1	4		1						15	24.03	0.80
August	4	9	19	12	2	1	1				48	25.50	0.43
October ...			6	5	3	1	5	1	1	1	23	27.76	0.88
1974													
January ...	1	8	16	13	13	7	2	2		1	63	26.71	0.45
February ..			5	5	4	5	3	2	1	5	30	28.53	0.88
March		9	52	80	58	22	11	5		1	238	26.89	0.17
April			9	34	22	23	7	3	1	1	100	27.55	0.26
July	1		2	5	1						9	25.94	0.47
August	24	8	3	—	—	1					36	23.25	0.26
Total	56	115	254	400	573	437	297	200	66	22	2 421		

Table 8. Length distribution of herring (in per cent) from purse seine catches in Lindåspollene, 1970–74.

Year	Length, cm																					n
	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	
1970						1.2	35.7	42.9	15.5	4.7													84
1971							6.4	6.8	4.3	1.7	11.5	26.7	22.2	12.4	4.3	2.1	0.4	0.4	0.4	–	–	0.4	234
1972	1.4	47.5	46.2	1.4	0.7	–	–	–	0.7	0.7	–	0.7	–	–	0.7	–							139
1973					64.0	25.0	1.0	1.0	–	–	–	1.0	–	–	–	–	1.0	4.0	2.0	1.0	–	–	100
1974									6.0	32.0	38.0	6.0	–	–	1.0	3.0	2.0	1.0	1.0	6.0	3.0	1.0	100

Table 9. Growth estimates (true mean) for the Lindås herring during the first four years of life (L_1 - L_4), with 95% confidence intervals of the means (C.I.).

Year-class	Length, cm							
	L_1	± C.I.	L_2	± C.I.	L_3	± C.I.	L_4	± C.I.
1970	9.5	0.4						
1969	9.1	0.2	16.2	0.4				
1968	11.2	0.7	19.5	0.8	24.3	0.6		
1967	10.9	0.6	19.0	0.7	23.8	0.6	25.2	0.5
1966	10.0	0.1	16.5	0.2	21.9	0.1	25.4	0.1
1965	11.0	0.3	19.3	0.5	22.5	0.4	24.8	0.3
1963	10.1	0.4	17.3	0.7	21.0	0.9	23.8	0.5
1962	10.0	0.3	16.3	0.4	20.3	0.5	23.2	0.4

Table 10. It should be noticed that the data for the 1961 and 1964 year classes were very scarce, and the estimated length-at-age for these year classes may therefore not be precise. The entries in the table along the diagonal, i.e. length at capture for the various year classes, refers to individuals caught during the last quarter of the year only, when annual growth is terminated. The table shows that the length increments for individuals older than 4 years in 1971 were small, indicating unfavourable growth conditions.

The data in Table 10 were plotted in a Walford diagram (Fig. 6) of L_{t+1} versus L_t, and the regression line:

$$L_{t+1} = 10.38 + 0.66 L_t$$

Table 10. Growth estimates (true mean) for the Lindås herring from the 1971 material.

Year-class	Length, cm											n
	L_1	L_2	L_3	L_4	L_5	L_6	L_7	L_8	L_9	L_{10}	L_{11}	
1970	9.5	15.6										19
1969	9.1	16.2	20.3									96
1968	11.2	19.5	24.3	26.0								25
1967	10.9	19.0	23.8	25.2	26.8							27
1966	10.0	16.5	21.9	25.4	27.5	27.5						331
1965	11.0	19.3	22.5	24.8	27.0	28.6	28.9					55
1964	10.1	17.8	22.0	23.8	25.8	27.6	29.0	29.8				3
1963	10.1	17.3	21.0	23.8	25.5	27.2	28.9	30.0	30.4			22
1962	10.0	16.3	20.3	23.2	23.8	26.0	27.4	28.9	30.2	30.2		39
1961	9.8	15.9	20.6	24.8	25.0	26.2	27.0	28.6	29.7	30.5	30.5	9

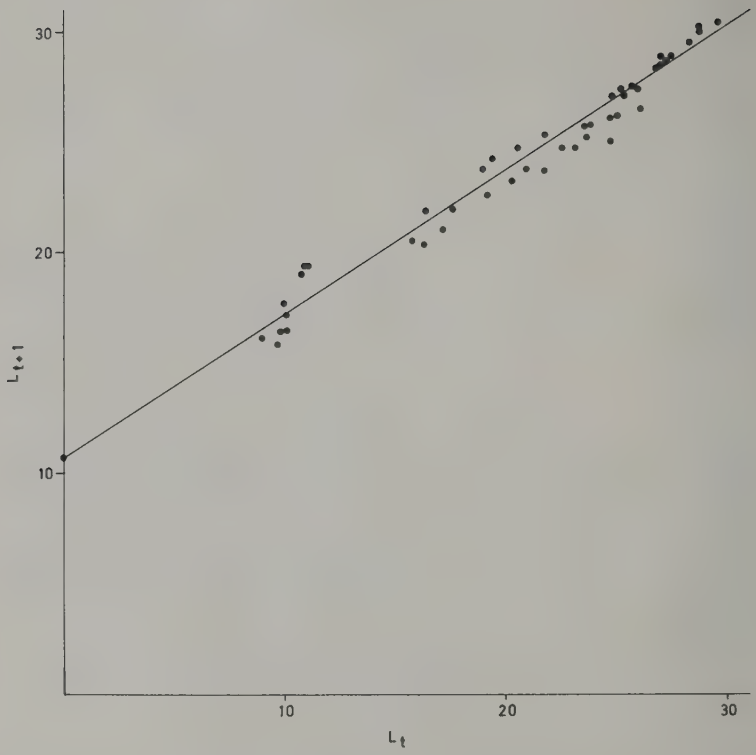

Fig. 6. Walford plot of back calculated lengths from scale readings.

could be fitted by the method of least squares. The regression line was used to determine $L\infty = 30.49$ and $t_0 = 0.035$, and the von Bertalanffy growth equation for the Lindås herring was determined as:

$$L_t = 30{,}49\ (1 - e^{0.416\,(t - 0.035)}).$$

The growth curve represents the mean growth of the Lindås herring well during the first four years of life (Fig. 7), but from the fifth year on the calculated growth was too high. The «strange» herring had a considerably higher growth rate during the first four years of life than the Lindås herring, whereas the Lusterfjord herring (Aasen 1952) had a slower growth (Fig. 7).

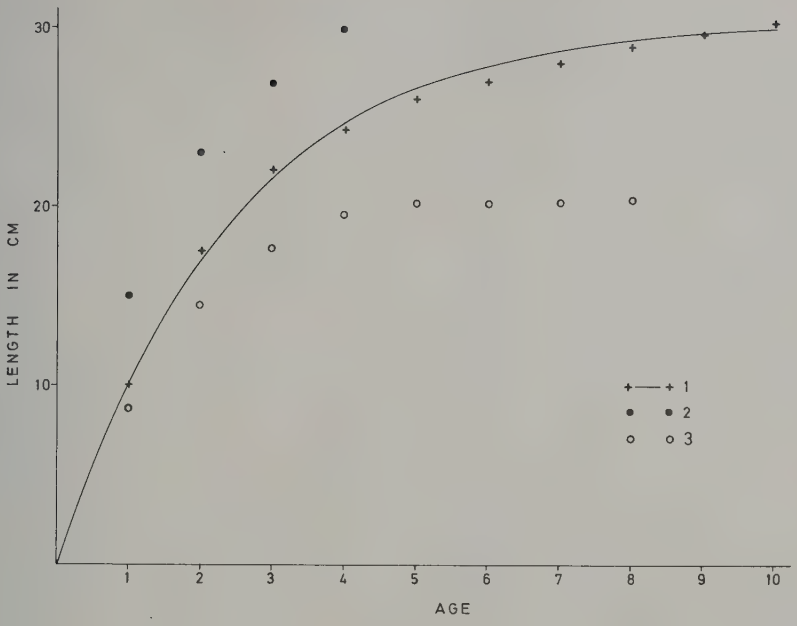

Fig. 7. Von Bertalanffy growth curve for the Lindås herring (1), and length/age plots for the «strange» herring (2) and the Lusterfjord herring (3) from Aasen (1952).

WEIGHT, CONDITION FACTOR AND INTESTINAL FAT CONTENT

The weight of the herring from the gill net samples ranged from 70 to 300 g (Table 11), and about 60% of the individuals weighed from 150 to 200 g. The monthly mean weights during 1973, when the 1969 year class dominated in the samples, were considerably lower than during the preceding years.

The 1966 year class, which dominated during 1970, 1971 and 1972, showed distinct seasonal variability in weight, with minima during the first and maxima during the last quarters of the years (Table 12).

In 1971 the herring did not attain the same weight as in 1970 whereas a pronounced increase in weight took place during 1972. This is an indication that the conditions for the herring in Lindåspollene during 1971 were poor which explains the slow growth during 1971.

The weight/age curve was typically sigmoid (Fig. 8), and the natural logarithms therefore yielded two reasonably straight lines, intersecting at the fourth year of age. This is the age of maturity for the majority of the Lindås herring, and the change in weight increase may therefore be related to the ripening of the gonads.

Table 11. Weight frequency distribution of Lindås herring, 1970–1974.

Month	Weight in g																n	Mean
	<100	100	110	120	130	140	150	160	170	180	190	200	210	220	230	>230		
1970																		
October								5	2	4	1	1	–	–	1	1	15	181
November			1	1	1	1	9	7	13	16	11	15	6	2	3	21	107	196
1971																		
January					1	8	12	12	14	4	6	3	3	3	4	1	71	173
February	2	–	–	2	–	1	3	1	5	1	2	2	1	2	2		24	170
March	1	1	3	3	11	10	23	26	18	9	11	13	3	9			141	165
April				1	6	6	12	15	22	9	3	1	1	2	–	1	79	164
May				1	3	14	22	18	23	9	1	2	1	1			95	160
June				1	5	7	24	30	10	8	10	3	6	–	–	3	107	166
July			3	–	3	1	4	5	4	3	1	1	–	1	–	1	27	160
September			2	1	1	2	6	10	12	7	2	9	8	2	5	4	71	183
October			2	–	2	2	2	–	–	3	–	1	3	–	–	4	19	185
November	1	7	7	5	10	11	16	13	17	17	10	18	7	8	–	4	151	173
1972																		
January			4	7	5	15	34	29	31	25	22	13	12	2	1		200	168
March			1	1	1	4	10	4	5	5	2	1	2	–	1		37	163
April		2	3	–	1	1	1	–	–	3	–	–	–	2	–	1	14	157
May					1	3	1	5	3	3	2	–	2	–	2		22	173
August			3	6	9	2	2	6	5	8	6	7	6	8	2	8	78	182
October			1	9	2	3	–	–	1	2	–	2	1	1	–	1	23	151
November	2	5	5	10	5	8	6	11	6	14	11	13	13	8	12	13	142	176
1973																		
January		4	3	2	2	3	1	3	1	–	1	1	1	1	–	1	24	146
February		3	2	3	–	3	3	2	1	1	–	–	1	1	–	2	22	153
March			7	12	12	2	8	2	5	3	3	1	2	1			58	144
April	2	8	9	2	1	–	2	–	–	1							25	113
July			6	3	1	1	2	1	–	–	–	–	1				15	131
August	6	1	3	5	12	9	5	3	1	1	–	1	–	–	1		48	132
September	7	7	12	23	21	17	16	6	6	3	–	1	–	2			121	132
October			1	1	3	1	3	1	3	2	2	1	1	1		3	23	176
1974																		
January	4	6	11	12	6	5	7	6	1	–	3	1	1				63	131
February		1	3	3	2	4	4	2	2	2	–	1	1	3	2		30	159
March	4	14	24	42	44	35	23	26	9	3	4	4	3	1	–		236	136
April			2	5	21	11	23	12	4	6	7	2	5	1	1		100	155
July			1				2	1	–	3	2						9	166
August	25	7	2	–	2												36	87
Total	54	66	120	161	194	190	287	262	224	175	123	118	91	62	37	69	2 233	

Table 12. Mean weight of the 1966 year class in the Lindås herring, 1970–1974.

Month	Mean weight	n
1970		
October	175	13
November	185	78
1971		
January	160	41
February	168	13
March	160	76
April	160	55
May	161	63
June	163	87
July	164	16
September	177	36
October	173	4
November	165	59
1972		
January	161	88
March	156	28
May	155	7
August	210	21
November	194	62
1973		
January	202	9
March	182	7
1974		
March	158	9
April	194	9

A regression line for weight and length data for 2233 herring (Table 13) in logarithmic transformation was determined as:

$$W = 0.011\ L^{2.9025}$$

The regression line is plotted in Fig. 9. The 95% confidence interval for the slope of the regression line (2.9025) was ± 0.1392, and the hypothesis of isometric growth, i.e. the slope was not significantly different from 3, could no be rejected.

The condition factor (FULTON 1911):

$K = W/L^3$ (W in g L in cm)

is a measure of weight per unit volume under the assumption of isometric growth, and the larger the K, the better is the «condition» of the fish.

The condition factor was determined for all the individuals collected during 1970–1974 (Fig. 10). The highest values usually occured during

Table 13. Length-weight relationship of Lindås-herring, 1970–1974.

g	Length, cm																			
	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31
10	5	2																		
20	8	7	14	3																
30			1	15	9	1														
40					1	3	4	1												
50							11	8	1											
60							6	29	7		1									
70								10	16	2	1									
80									14	9	1	2								
90									3	11	3	7	5							
100										1	5	3	29	20	1					
10											3	6	33	36	10					
20											2	6	20	72	45	8				
30												2	9	76	77	21	2			
40													3	36	86	59	9	2		
50														15	72	120	22	4		
60														5	42	134	36	10	3	
70														1	25	77	78	34	4	
80														1	11	35	60	38	11	
90															3	23	38	47	19	
200															2	18	26	32	27	4
10																3	17	35	24	5
20																	10	19	16	7
30																	4	10	19	7
40																	3	8	7	11
50																		5	8	3
60																		—	3	4
70																		—	2	3
80																		1	4	4
90																			1	2

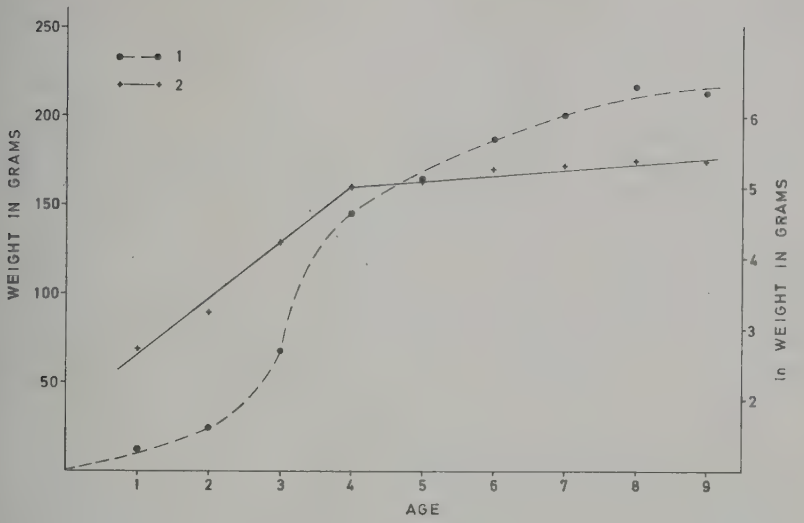

Fig. 8. Weight/age curves for the Lindås herring.

August–October, but there were distinct differences from year to year. Thus, it appears that 1970 and 1972 were particularly «good» years, whereas 1971 and 1973 had considerably lower condition factors during early autumn. A decrease in the condition factor could be observed already in October, and the minimum was usually reached in January. Then there was a rapid increase, culminating in March, and subsequently a decrease until the annual minimum was observed in May. On the average there was a decrease in the condition factor of about 15% from the autumn maximum to the May minimum, but from autumn 1970 to May 1971 the decrease was more than 20%. This decrease in weight reflects changes in body fat and sexual products, and therefore the annual variability in calorific content must be considerably higher than the variability in weight.

The rapid changes in the condition factor during the first quarter of the year coincides with the change from maturity stage IV to stage V and VI, i.e. the period of the most rapid growth of the gonads (Aasen 1952).

The amount of fat deposited on the intestines is commonly used as an indicator of quality in the marketing of herring, and the intestinal fat is thus another measure of the condition of the fish. In the present investigation the amount of intestinal fat was classified in accordance with Aasen (1952). The intestinal fat content was highest in July–August, when about 80–90% of the individuals had moderate fat content (Fig. 11). Through the autumn and winter there was a rapid decrease in the intestinal fat, and less than 10% of the individuals showed traces of fat during spawning in late March. After

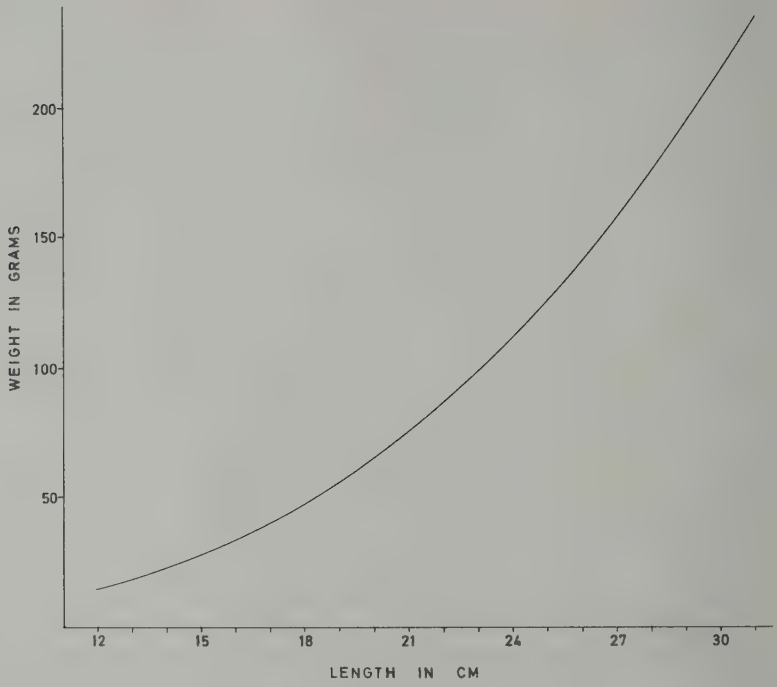

Fig. 9. Weight/length curve for the Lindås herring.

the spawning the herring very quickly startet to deposit intestinal fat again, and already in May had 45% of the individuals a moderate amount of fat.

It is interesting to note that the amount of intestinal fat started to decrease from August–September which indicates that the herring already then could not find sufficient food for maintenance metabolism, but had to utilize deposited fat as a source of energy.

There were some differences among the years in amount of intestinal fat; thus, it appeared that the decrease in autumn started one month earlier in 1971 than i 1972 and 1973. However, the inaccuracy of the classification method for intestinal fat prevents more stringent testing of annual differences.

MATURITY, FECUNDITY AND SPAWNING

The maturity stages were determined by the method of JOHANSEN (1919) which has been slightly modified and adopted for the Atlanto Scandian and

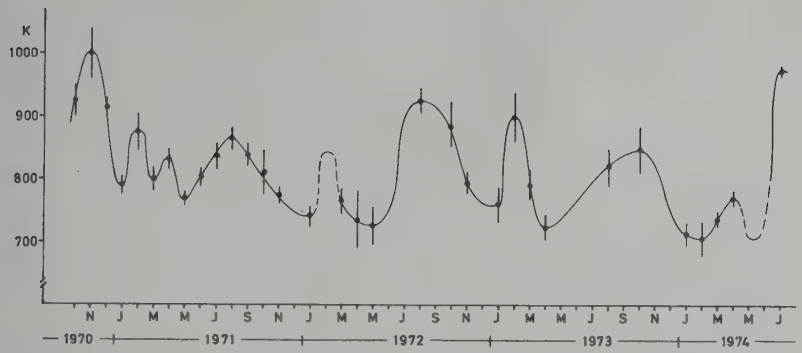

Fig. 10. Variation in the condition factor of the Lindås herring during 1970–1974. Vertical lines: 95% confidence intervals.

for the North Sea herring stocks (ANON. 1963). In a qualitative classification scheme there is always an element of subjectivity on the part of the investigator, which introduces an added variance component in the data. In the present study this component has been minimized because all the maturity stage determinations have been made by one of the authors (O.D.) who has considerable experience with the method.

The overwhelming majority of the herring caught with gill nets were mature or maturing (Table 14), only 3.6% were in stage II and none in stage I. The size selectivity of the nets is the principal reason for this, but there are also indications that the migration pattern of the immature herring may be different from that of the mature stock (ØSTVEDT *et al.* 1974). Mature and immature herring will therefore not be caught together in the nets.

Maturity stage III appears in May–June and dominates from July–August until October (Table 14), and stage IV dominates from October until February. During February–March the herring pass through stage V, and the majority of the specimens were in stage VI, i.e. with fully ripe gonads, at the end of March. High percentages of spent herring (Stage VII) were rarely encountered, but recovering spent herring (stage VIII) dominated the samples during the period May–July. The scarcity of samples during the period May–August prevents accurate determinations of maturity stage distribution during this period.

Maturity stage IV was observed for about four months, stages III and VIII about three months, whereas the stages V–VII lasted only about two to four weeks (Fig. 12 A). This maturity cycle is very similar to that of the Atlanto Scandian herring (Fig. 12 B), but each maturity stage was reached about one month later in the year.

Thus, spawning in Lindåspollene occurred in late March, which coincides with the spawning time for other local west Norwegian herring stocks,

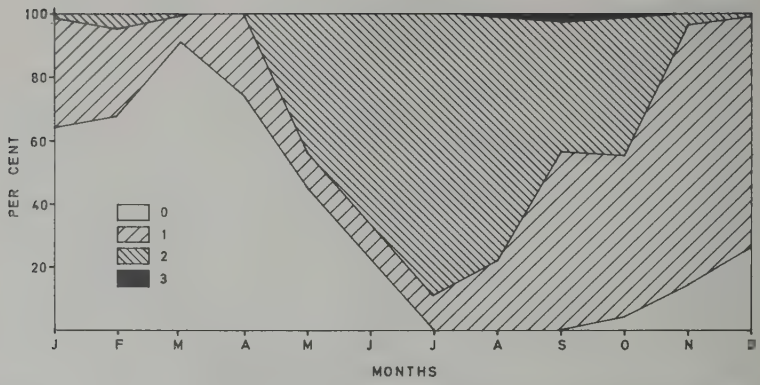

Fig. 11. Mean percent distribution in amount of intestinal fat through the year in the Lindås herring. 0: no fat, 1: traces of fat, 2: moderate fat, 3: much fat.

e.g. Heiamarkspollen and Fjellspollen (Anon. 1964) and Lusterfjorden (Aasen 1952).

Although there was a general seasonal trend in the maturity cycle of the herring in Lindåspollene as outlined above, there were also distinct differences among the years, particularly concerning maturity stages V and VII. It is noteworthy also, that a few specimens in stage VI were found in October–November 1971. Autumn spawning herring have also been observed in other polls in the Bergen area (Anon. 1964).

There were 53,2% males and 46.8% females in the total gill net catch during 1970–1974, and the males dominated in the majority of the samples. However, a t-test for the paired samples showed that the difference in sex composition was not statistically significant ($t = 1.49$, $0.10 < p < 0.20$).

Fecundity was determined on 117 herring ranging in length from 24 to 31 cm. The mean number of eggs per ovary ranged from 35459 at 24 cm to 51615 at 31 cm, but there were large variabilities in fecundity within length groups. An analysis of variance on log transformed data (Table 15) showed that the variance component among length groups was significant on the 95% level of probability, and a regression line was therefore fitted. The regression equation was:

$N = 363.33\ L^{1.42}$

where N = fecundity, L = length in cm. The correlation coefficient was low ($r = 0.4390$) but statistically significant at the 99% level of probability.

The slope of the regression line differed quite distinctly from the results of previous investigations on the fecundity of herring. Thus, Baxter (1959) found slope values ranging from 3.8417 to 4.3290 in three different North Sea stocks and Atlanto Scandian herring, and Kändler and Dutt (1958)

Table 14. Maturity stages (%) of Lindås-herring 1970–74, per month, gill nets.

Month		Stages								n
		I	II	III	IV	V	VI	VII	VIII	
Oct.	1970			60.0	33.3	6.7				15
Nov.	»			1.8	98.2					116
Jan.	1971				95.7	4.3				71
Feb.	»			4.2	58.3	37.5				24
Mar.	»		1.3	—	5.1	17.3	75.0	1.3		156
Apr.	»						7.5	58.7	33.8	80
May	»			9.0	—	—	3.3	—	87.7	90
June	»			10.0	—	—	—	—	90.0	107
July	»		3.8	88.5	—	—	—	—	7.7	26
Sept.	»		1.5	77.1	21.4					70
Oct.	»			15.8	73.6	5.3	5.3			19
Nov.	»		1.2	4.0	92.0	0.7	0.7	0.7	0.7	150
Jan.	1972		0.5	0.5	98.0	0.5	—	0.5		200
Mar.	»				17.0	55.3	26.6	1.1		94
Apr.	»						85.7	14.3		14
May	»			13.6	—	4.5	—	4.5	77.4	22
Aug.	»		24.0	24.0	52.0					75
Oct.	»			65.2	34.8					23
Nov.	»		0.7	5.0	92.9	1.4				141
Jan.	1973		12.0	32.0	52.0	—		—	4.0	25
Feb.	»		4.8	4.8	85.6			—	4.8	21
Mar.	»					7.5	84.6	7.8		65
Apr.	»					24.0	72.0	4.0		25
July	»		40.0	13.3	—	—		—	46.7	15
Aug.	»		27.5	45.0	27.5					40
Oct.	»			87.0	13.0					23
Jan.	1974		28.6	1.6	50.8	14.2	—	1.6	3.2	63
Feb.	»		3.3	6.7	73.4	13.3	—	3.3		30
Mar.	»		5.1	3.4	7.2	65.7	16.5	1.7	0.4	236
Apr.	»					5.0	95.0			100

found slope values ranging from 3.465 to 5.063 in three Baltic and two North Sea stocks. The size of the gonads in fishes is generally an isometric function of length, i.e. the fecundity is proportional to the cube of the length (Bagenal and Braum 1968), and a formula of the form:

$F = a + b\ L^3$

would therefore be a more realistic representation of the relationship between length and fecundity. Applying this formula to the data on the Lindås herring by the method of least squares, the regression equation:

$F = 20843 + 0.97\ L^3$

was estimated.

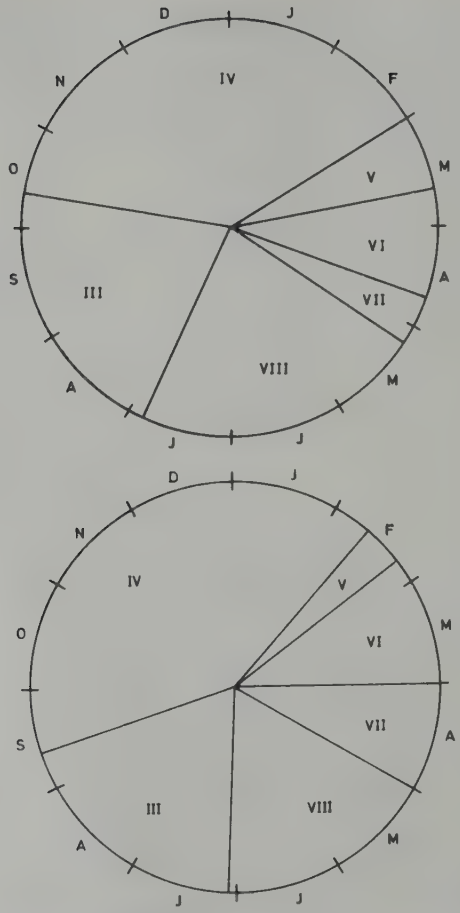

Fig. 12. Annual maturation cycle in the Lindås herring (above) and in the Atlanto-Scandian herring (belowe).

The two regression lines were not distinctly different (Fig. 13), but the line based on the cube of lengths is probably preferable.

The mean weights of the gonads collected during January, February and March of 1971 represented 12.9% ± 1.2%, 16.3% ± 1.3% and 19.3% ± 1.4% of the total body weight, respectively. A mean weight loss of about 20% during spawning must therefore be expected, and this compares favourably with other investigations on herring (Aasen 1952).

Table 15. Analysis of variance on fecundity. Herring ranging in length from 24 to 31 cm (8 length groups).
Data in log-transformation.

Source of variation	df	SS	MS	F
Among length classes	7	0.2576	0.0368	4.9066
Linear regression	1	0.1860	0.1860	15.6303
Deviations from regression	6	0.0716	0.0119	1.5866
Within length classes	99	0.7076	0.0075	

Syslakvågen (Fig. 1) has long been recognized as a spawning area for the Lindås herring (Dahl *et al.* 1973), but the investigations during 1970–1974 revealed considerable annual variability in the success of the spawning. Massive spawning was observed in Syslakvågen on 23 March 1971 and 27 March 1972 in depths from 0 to about 4m (Fig. 14). The eggs, which were clearly visible from the surface, were attached to algae, pebbles and rocks, distributed over an area of about 2 500 m^2. No eggs were observed on the spawning ground in 1973 and only a small number in 1974.

In 1971 herring larvae were collected with a Clarke-Bumpus plankton sampler in the surface waters on the spawning ground, and the maximum number of larvae, 43.5 individuals/m^3, was observed on 20 April. In 1972 larvae were observed from 16 April, reaching a maximum of 140.8 individuals/m^3 on 25 April. In 1973 no herring larvae were observed in Lindåspollene on larval surveys carried out until the month of July. Thus, there are indications that the spawning was a failure in 1973, and this hypothesis is supported by the fact that no 0-group herring were found in a purse seine catch from September 1973, nor I-group in a sample from September 1974 (Table 8).

In a detailed study of spawning and larval ecology of the Lindås herring Furevik (1976) observed spawning in Syslakvågen in 1974, but not in 1975. The highest number of larvae on the spawning ground in 1974, 151.27 individuals/m^3, was observed on 17 April, i.e. 20 days after spawning.

DISCUSSION AND CONCLUSIONS

The herring in Lindåspollene can be distinguished from neighbouring stocks by vertebral counts or growth pattern. However, both of these parameters are subject to phenotypic variation, and genetic studies must therefore be performed in order to further describe the racial identity of the stock. The component of fast growing herring occurs mainly as young

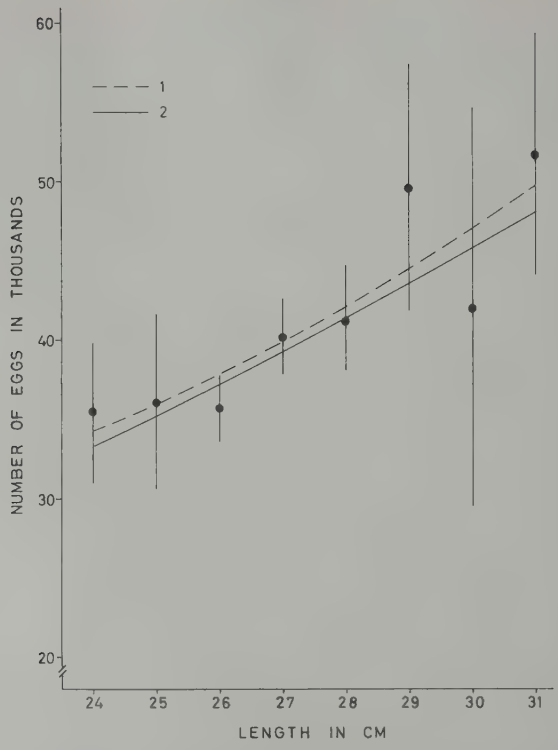

Fig. 13. Fecundity/length curves of the Lindås herring. 1: $N = 20843 + 0.97 L^3$, 2: $N = 363.33 L^{1.42}$

mature individuals. It seems reasonable, therefore, to conclude that the «strange» herring spends only shorter periods of their lives within Lindåspollene.

The migration of the herring stock within Lindåspollene seems to follow a standard pattern which could be compared with seasonal migration found in herring stocks in the open ocean as described by Harden Jones (1968). The feeding migration in spring is particularly directed towards Straumsosen, but a part of the stock moves also to the southern shallow part of Spjeldnesosen. On the basis of the hydrographical data alone it is difficult to explain this seasonal migration. A study of zooplankton during 1971–1972 revealed, however, that the spring migration coincided with a maximum of zooplankton biomass in Straumsosen and in the southern part of Spjeldnesosen in April (Haug 1972). In the sentral parts of Spjeldnesosen a spring

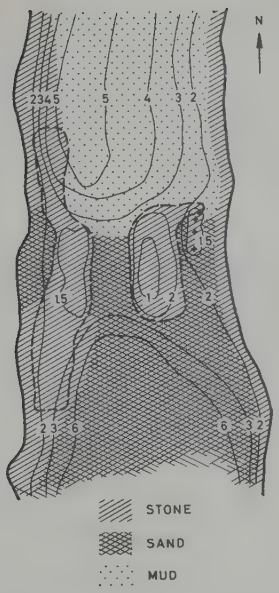

Fig. 14. Depth contour lines and bottom types at the spawning ground in Syslakvågen.

zooplankton maximum was not observed. There were also local differences in the composition of the zooplankton, *Calanus finmarchicus* being more abundant in Straumsosen (Ellingsen 1973). Thus, the feeding migration seems to be related to differences in quantity and composition of zooplankton within Lindåspollene.

The majority of the zooplankton during late autumn and winter was concentrated in the deeper layers of Spjeldnesosen (Haug 1972), i.e. in the overwintering area for the herring. Attempts to catch herring at daytime during the overwintering period have not been successful, and therefore one cannot conclude whether feeding takes place or not.

Emigration of part of the Lindås herring stock to the neighbouring fjords might be expected (Anon. 1964). The differences in the environmental and feeding conditions between the outside fjord system and Lindåspollene would probable be reflected in the growth pattern as determined from scale readings, but such changes in the growth were never observed. It seems likely, therefore, that the emigrated herring do not return to Lindåspollene.

The local herring stock in Lindåspollene is characterized by large fluctuations in the relative strengths of the year classes, with a rich year class

emerging every 3–4 years. The present investigation has shown that there were parallel fluctuations in the success of the spawning as determined from observations on the spawning grounds in Syslakvågen and from larval surveys (Furevik 1976). The prespawning aggregation of the herring in the northern part of Spjeldnesosen was observed each year, but in both 1973 and 1975 (Furevik 1976) the herring did not spawn in Syslakvågen. Estimates of spawning stock size are not available, but age composition data of the prespawning stock in 1973 revealed that the strong 1969 year class dominated, and one would therefore expect a relatively large spawning stock. Thus, the spawning failure in 1973 indicates that success of spawning is not directly related to the spawning stock size. Environmental conditions on the spawning grounds may, however, have a major effect on the success of spawning. In late March 1973, when the spawning failed, i.e. the mature herring did not enter the spawning grounds in Syslakvågen, the salinity at 80 cm depth was only 15.0–17.0‰. (Ellertsen 1975). Also Runnstrøm (1941) demonstrated for the Atlanto Scandian herring that environmental conditons are important during spawning, and that the herring only deposit their eggs at certain hydrographic conditions. The spawning area in Syslakvågen is shallow, and therefore it is conceivable that the environmental conditions are affected by short term variability in meteorological parameters such as temperatures and precipitation. However, there was no relationship between the strength of the year classes during the period 1959–1974 and the temperature and the precipitation during the first three months of the respective years.

The success of spawning seems to be one of the major factors determining the strength of the year classes, but there are indications that factors affecting eggs and larvae may be equally important. Thus, the number of eggs deposited on the spawning grounds in 1971 was at least as high as in 1972, but the highest density of larvae on the spawning ground at the time of hatching in 1971 was 43.5 individuals/m^3 compared to 140.8 individuals/m^3 in 1972. Observations from purse seine samples during 1971–1974 (Table 8) indicated that the strength of the 1971 year class was insignificant compared to the 1972 year class.

The spawning in 1974 was less successful than in 1971 and 1972, but the number of larvae on the spawning ground at the time of hatching was about the same as in 1972 (151.3 individuals/m^3). Thus, the effect of a successful spawning may be reduced by high egg mortality. Furevik (1976) observed predation on the herring eggs by cod, pollack and haddock, and he found that egg mortality was correlated with egg density.

The investigations during 1971–1974 indicate that the very considerable variability in the strength of the year classes in the Lindås herring stock is primarily related to success of spawning in Syslakvågen and to the biotic and abiotic conditions on the spawning grounds. These relationships will be the

object of detailed studies in the future research programme in Lindåspollene. The time when the yolk sac has been resorbed has long been considered a critical period in the life of fish larvae (HJORT 1914, 1926) because the absence of suitable and sufficient food organisms may lead to mass starvation. SOLEIM (1942) reported on observations of large numbers of dead herring larvae in samples from the spawning grounds of the Atlanto Scandian herring.

Abundance of larvae at the egg yolk stage has often been used as an index of spawning stock size (SAVILLE 1964). The observation made in Lindåspollene both on the success of spawning and the larval abundance, shows that further studies on the relationship between spawning stock size and larval abundance are greatly needed.

The herring larvae in Lindåspollene may be subjected to considerable fluctuations in the amount of food organisms from year to year. HAUG (1972) found that the zooplankton biomass during the months of March and April was about twice as high in 1972 as in 1971, and ELLINGSEN (1973) found the same difference in the number of zooplankton organisms. Thus, the 1971 year class experienced very poor food conditions at the larval stage, which may be an additional source of reduction of the year class. The poor plankton conditions in 1971 are also reflected in slow growth of all year classes, and in that there was no increase in the mean weight during 1971. Similarly, the condition factor and the amount of intestinal fat during 1971 indicated poor feeding conditions.

The zooplankton community in Lindåspollene is strongly dominated by small copepods. The mean biomass (ashfree dry weight) during the period April–September 1971 for *Pseudocalanus elongatus, Temora longicornis,* and *Oithona similis* was 87.5, 43.7 and 43.7 mg/m^2, respectively, whereas the dominant larger zooplankton organism, *Calanus finmarchicus,* had a mean biomass of 19.7 mg/m^2 (ELLINGSEN 1973). Assuming that the composition of the zooplankton in the watermasses reflects the diet of the herring (SAVAGE 1931), the food of the Lindås herring would consist mainly of small organisms. The energy expenditure related to feeding on the small prey may reduce their relative importance as food organisms, which might explain the slow growth of the Lindås herring compared to the North Sea herring stocks and Atlanto Scandian herring. In these herring stocks *Calanus finmarchicus* constitutes the most important food organisms (RUDAKOVA 1956, CUSHING 1962).

Lindåspollene is characterized by low temperatures (5–3°C) in the water masses deeper than 25–30 m, and the hydrographic investigations during 1971–1974 revealed only small seasonal fluctuations in the temperatures at these depths (AURE 1972, WESTERGAARD 1975). During most of the year the major part of the herring stock was at day time distributed at depths exceeding 30 m, i.e. in water masses 3–4°C colder than the deep water of the

Norwegian coast and fjords (Eggvin 1940, Sælen 1962). Thus, the herring are most of the year exposed to low temperatures and one might expect reduce growth rate even during good feeding conditions. The part of the Atlanto Scandian herring, which are living under the most extreme temperature conditions, e.g. the northern growth type, had reduced growth rate as compared with the more southern component of the stock (Østvedt 1965).

Studies on local Norwegian herring stocks indicate, however, that food conditions play an important part in the growth of the herring. The Lusterfjord herring (Aasen 1952) lives in water masses 2–3°C warmer than the water in Lindåspollene, but it has a very slow growth rate. The zooplankton conditions in the two areas are, however, quite similar, thus *Calanus finmarchicus* comprised about 2% of the total number of organisms in Lindåspollene (Ellingsen 1973) and about 3% in Lusterfjorden (Aasen 1952).

The zooplankton of both areas was dominated by small copepods, e.g. *Pseudocalanus elongatus, Acartia spp., Temora longicornis, Oithona spp,* and *Paracalanus parvus.* It seems, therefore, that the slow growth of the herring in Lusterfjorden and in Lindåspollene is related to the composition of the zooplankton community rather than to the temperature of the water masses. This conclusion agrees well with Cushing (1962) who demonstrated increased growth of the North Sea herring after 1950 as *Calanus* became more predominant in the zooplankton.

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FOOD AND FEEDING OF YOUNG HERRING LARVAE OF NORWEGIAN SPRING SPAWNERS

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ABSTRACT

BJØRKE, H. 1978. Food and feeding of young herring larvae of Norwegian spring spawners. *Fisk.Dir. Skr. Ser. HavUnders.*, *16*: 405–421.

The gut contents of young herring larvae sampled each hour from 3 to 9 April 1967 at three depth intervals around a floating drogue were examined to study their feeding.

Copepod eggs constituted more than 90% of the food items. Feeding started shortly after sunrise within the same hour in the depth intervals 25–5 m, 30–50 m and 75–55 m. Mean length increased with diminishing yolk sac until absorption when mean length decreased. The latter could indicate lack of suitable food.

The mean gut content of feeding larvae did not increase until after absorption of the yolk sac.

Larvae from the deepest strata had less gut contents than the others, probably because a lower percentage of them had absorbed yolk sacs.

A high percentage of larvae feeding during day-time contradicted total defecation due to capture.

No correlation was found between numbers of *Calanus* eggs in the guts and in plankton. Larvae containing *Calanus* nauplii had more assorted gut contents than larvae containing *Calanus* eggs.

The critical period concept is discussed.

INTRODUCTION

Due to the widely held opinion that year-class strength of herring and other fish species is determined during early life, many investigations have dealt with larval stages.

Analyses of food and studies of feeding behaviour have drawn great interest. Several authors have compared the composition of the gut contents of herring larvae with the surrounding plankton, and attempts have been made to estimate the amount of food required for survival (for references see BLAXTER and HOLLIDAY 1963, BLAXTER 1965, SAVILLE 1971, SCHNACK 1972 and MAY 1974).

Most of these investigations, however, dealt with herring larvae from the North Sea and the Baltic and rather little is known about Atlanto-Scandian

herring larvae. The plankton at the spawning grounds of this stock is dominated to a much greater degree by *Calanus finmarchicus* than the plankton at the spawning grounds of other stocks. This reduces the diversity of the available food and makes the larvae more or less dependent on one type of food organism.

DRAGESUND (1970) assumes the coincidence in time between occurrence of suitable food and hatching of herring larvae to be the most important environmental factor controlling year-class strength during early larval development of Norwegian spring spawners. The aim of the present investigation was to study a) the food composition of Norwegian spring spawners, b) factors affecting their gut contents, c) selection of food particles, and if possible d) to discover any critical periods.

MATERIALS AND METHODS

The Institute of Marine Research, Bergen, carried out extensive investigations at the spawning grounds of economically important fish as part of the International Biological Programme during the years 1967–1971. The material used in the present work was selected from an experiment to study the drift of herring larvae off the West coast of Norway (DRAGESUND and NAKKEN 1971).

Sampling was carried out 3–9 April 1967 in a larval concentration marked by a floating drogue. The sampling area around the floating drogue covered 1 nautical mile^2. Larval samples were taken almost every hour as oblique hauls with three permanently open Clarke-Bumpus plankton samplers equipped with nylon nets of 500 μ mesh size. Total towing time was 20 minutes, and the samplers were raised in 5 m steps each 4 minutes. The sampling intervals were 25–5 m, 50–30 m and 75–55 m, and the towing speed was 1.5–2 knots. Plankton samples were taken at noon and midnight with Clarke-Bumpus plankton samplers equipped with nylon nets of 90 μ mesh size. The procedure was the same as for larval sampling, except for the use of the closing mechanism of the sampler and a reduction in towing time to 5 minutes.

Larvae from this material were selected for examination as follows (Table 1):

a) Larvae sampled during a 45 hour period from the 25–5 m depth interval to compare feeding intensity with time of day.
b) Larvae sampled during the last 24 hours of the previous period (a) from 50–30 m and 75–55 m to compare feeding intensity in all three depth intervals. Reduction in bottom depth below the floating drogue made this sequence incomplete.
c) Larvae from the plankton samples to compare gut contents and plankton composition, and larvae from the larval hauls nearest in time to these

plankton hauls to increase information when comparing gut contents and plankton composition.

The larvae were examined after six months preservation in 4% formaldehyde.

When present, 50 larvae from each sample were examined. The larvae varied in length from 6.4 to 12.4 mm with an average length of 9.8 mm.

The plankton samples were usually divided into subsamples of a hundredth with a plankton divider (WIBORG 1951), and two of these subsamples were then examined.

Reference to larvae caught at, for example, 1300 hrs., indicates that they were taken between 1230 and 1329. All times referred to are in local Norwegian time. When unspecified eggs and nauplii are mentioned, these are the eggs and nauplii of *Calanus finmarchicus*.

RESULTS AND DISCUSSION

COMPOSITION OF FOOD

Eggs of *Calanus finmarchicus* constituted in number 91.7% of the gut contents, while nauplii of the same species made up 4.6%. Eggs, nauplii and remains of copepod species other than *Calanus* constituted 2.9%.

BLAXTER (1965) reviewed work done on selection of food by herring larvae. He concluded that smaller larvae caught at sea most frequently contain copepod nauplii and eggs, mollusc larvae and some green food. However, a diet consisting of 92% copepod eggs as observed in the present work (Table 2), seems not to have been recorded from larvae of other stocks than Atlanto-Scandian herring. Other authors examining Norwegian spring spawner larvae also report a high percentage of *Calanus* eggs in the diet. SOLEIM (1942) found that *Calanus* eggs constituted the bulk of the larval diet, while RUDAKOVA (1971) found that they constituted 81.7 and 80.9% of the diet in 1966 and 1967 respectively. BJØRKE (1971) observed that *Calanus* eggs constituted in number 93% of the gut contents of young herring larvae.

SCHNACK (1972) examined the gut contents of herring larvae from the North Sea and the western Baltic. Although he found copepod eggs in the guts, no signs of digestion could be seen. This seems to be in contrast to the present investigation where the ratio of 1:2 empty shells to undigested eggs in the guts suggests that *Calanus* eggs are digested by the larvae. The finding of three empty shells and 59 undigested eggs in the foremost part of the guts shows that rather few empty shells are eaten by the larvae. Digestion of copepod eggs is also supported by a rather low percentage (3.3) of undigested eggs in the rectum. However, the findings of higher ratios of undigested to digested *Calanus* eggs as opposed to *Calanus* nauplii suggests that the digestion of eggs is slower than that of nauplii.

The largest food item, a *Balanus* sp. nauplius stage VI, was found in a larva 10.2 mm long.

Table 1. Numbers of examined larvae from the different depth strata.

Date, April	90 μ net															
	3	4		5					6	7		8		9		
Hour	24	15	16	01	02	12	14	24	13	01	12	24	14	01	13	Total
Depth, m																
25–5	7	17	12	21	30	27	35	53	9	–	1	–	5	1	2	220
50–30	–	–	–	–	11	15	–	17	30	5	6	20	5	15	4	128
75–55	–	–	–	–	53	–	7	2	–	23	5	–	–	–	–	90

Date, April	500 μ net																					
	4	5															6					
Hour	13	06	07	08	09	10	11	14	15	16	17	18	19	20	21	22	01	02	03	04	05	07
Depth, m																						
25–5	49	50	50	49	100	50	50	50	100	50	50	98	50	49	50	100	103	–	58	50	50	127
50–30	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	169	50	102	–	50	100
75–55	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	117	51	101	47	35	47

Date, April	500 μ net continued																				
	6												7				8		9		
Hour	08	10	12	13	15	16	17	18	19	20	21	22	01	02	10	11	09	12	12	16	Total
Depth, m																					
25–5	52	37	19	32	13	29	17	16	27	49	57	8	6	–	34	24	31	3	27	49	1 913
50–30	50	60	92	–	50	63	–	9	25	37	5	50	26	–	–	–	–	–	–	–	938
75–55	33	29	15	–	–	–	–	–	–	–	–	–	–	37	–	–	–	–	–	–	512

Table 2. Composition of food of 1707 herring larvae.

Undigested food			Digested food		
Types of food	Number	Percentage of total number	Types of food	Number	Percentage of total number
Calanus eggs	2 558	60.42	*Calanus* eggs	1 325	31.30
Calanus nauplii stages I–IV	58	1.37	*Calanus* nauplii stages I–IV	115	2.72
Calanus nauplii stages V–VI	7	.17	*Calanus* nauplii stages V–VI	11	.26
Microcal. nauplii	3	.07	Unidentified nauplii	11	.26
Balanus nauplii	1	.02	*Oithona* nauplii	1	.02
Unidentified nauplii	13	.31	Remains of copepods	67	1.58
Oithona eggs	17	.40	Unidentified objects	34	.81
Metridia eggs	1	.02			
Microsetella	9	.21			
Coscinodiscus	3	.07			

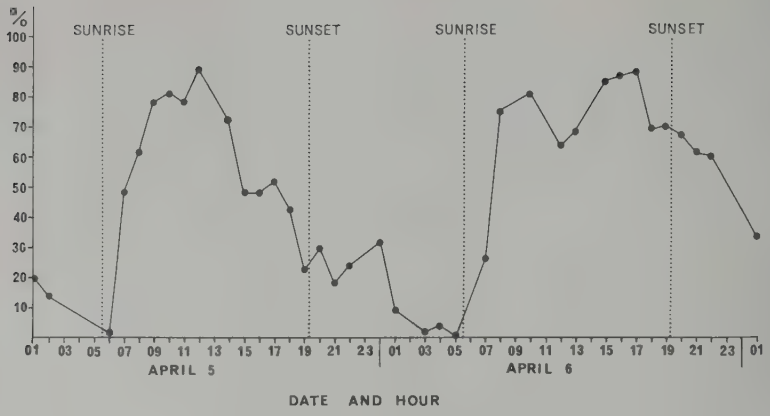

Fig. 1. Percentage of larvae from the 25 – 5 m hauls with undigested gut contents.

FEEDING ACTIVITY

Feeding started shortly after sunrise and declined at nightfall (Fig. 1).

Feeding started within the same hour in all three depth intervals. This activity correlates with observations made by Bainbridge and Forsyth (1971) on herring larvae in the Clyde. Assuming that the light threshold for feeding is the same at dusk and dawn, feeding activity should have ended at about 1830. Time available for feeding during a 24 hour period would therefore be 13 hours. This differs a little from the 16–18 hours available at 64° N as suggested by Blaxter (1966). He points out, however, that this is a maximum period based on light measurements taken at the surface; therefore the nearly total cloud coverage of the sky during the 45 hour period of the present investigation may have altered the time available for feeding.

The percentage of larvae with undigested gut contents was rather high at 2000 hrs. in the 25–5 m layer. Therefore, references later in this report to larvae caught during daylight include larvae caught between 0630 and 2029.

YOLK SAC SIZE AND LARVAL LENGTH

The mean length of the larvae increased with decreasing yolk sac size until absorption of the yolk sac, when the mean length decreased. This could indicate insufficiency of suitable food during that period.

The yolk sacs were classified as large, medium, small, absorbed and detatched. Fig. 2 shows the mean length, observed range and 95% confidence limits of 3770 larvae with the various yolk sac sizes. The range

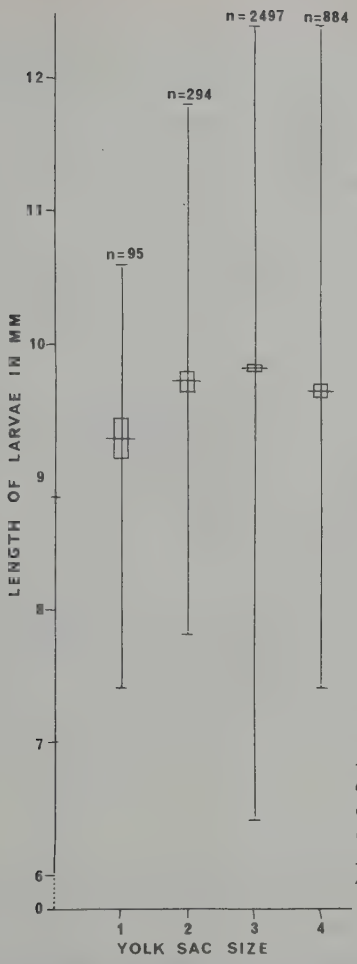

Fig. 2. Mean length, observed range and 95 % confidence limits of the herring larvae examined compared to yolk sac size. 1: large, 2: medium, 3: small, 4: absorbed.

within each stage overlaps to a considerable extent, yet t-tests show significant differences in mean length except for larvae with medium and absorbed yolk sacs. Similar overlapping was found by SOLEIM (1940) and RUDAKOVA (1971) in Norwegian spring spawners, and RUDAKOVA suggests that the overlapping shows differences in composition of the spawners. HEMPEL and BLAXTER (1963) and BLAXTER and HEMPEL (1963) found that herring females with large eggs generally produce larger and presumably stronger larvae with more yolk reserves at hatching. The overlapping in lengh of larvae with different yolk sac sizes might thus indicate differences in composition of the spawners as these authors suggest, but it might also indicate that feeding reduces absorption of the yolk sacs.

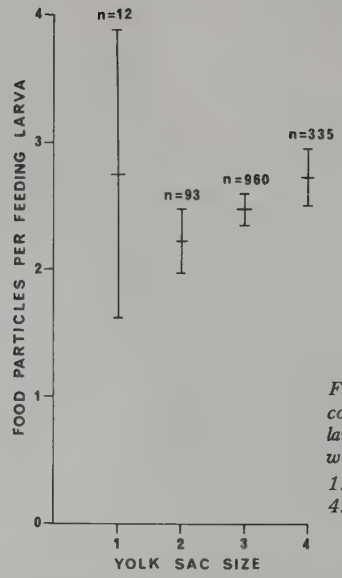

Fig. 3: Mean gut content and 95 % confidence limits of feeding larvae caught during daylight compared with yolk sac size.
1: large, 2: medium, 3: small, 4: absorbed.

Reduction in mean length with absorption of yolk sac, combined with the fact that the same larvae had the largest gut contents, (see later) could indicate insufficiency of suitable food for the larvae after absorpion of the yolk sac. BLAXTER and HEMPEL (1963) report shrinkage in body length of larvae starved under laboratory conditions.

FACTORS AFFECTING AMOUNT OF FOOD IN THE GUT

1. Yolk sac size

The percentage of larvae feeding increased with decreasing yolk sac size, but the mean gut content of feeding larvae did not increase significantly until absorption of the yolk sac.

Almost all authors who have studied feeding of herring larvae, report feeding before the yolk sac is absorbed. Of the 2150 larvae caught during daylight in the present work, 27% of those with large yolk sacs contained food, as did 61, 65 and 70% with medium, small and absorbed yolk sacs, respectively. When omitting the larvae without food, only larvae with absorbed yolk sacs had significantly greater gut contents than larvae with medium and small yolk sacs (Fig. 3).

This observation corresponds with that of ROSENTHAL and HEMPEL (1971) who found that herring larvae with yolk sacs were not successful in catching food items. The high mean gut content of the 12 larvae with large yolk sacs (Fig. 3) has to be disregarded because of few observations.

2. Depth

The highest mean gut content and the largest proportion of feeding larvae were found in the 50–30 m layer.

When studying the amount of gut contents in larvae from different depth intervals, only those caught during a short daylight period were examined to reduce the influence of changes in plankton. Therefore, only larvae caught between 0630 and 1229 on 6 April could be examined from the present material. The mean gut content per larva from the upper to the lowest depth strata was 1.1, 1.6 and 0.7 organisms, and the proportion of larvae with gut contents was 55, 56 and 39% respectively. All the differences between mean gut content were significant at the 5% level.

In the 25–5 m and 50–30 m plankton hauls taken at 1300 hrs. the numbers of *Calanus* eggs and nauplii were 4000 and 5600 organisms per m^3 respectively. Due to insufficient depth the 75–55 m plankton hauls had to be omitted that day. However, on the preceeding and following nights the densities of eggs added to nauplii were 1500 and 3200 per m^3 respectively.

It is questionable as to whether the number of food items in the different depth layers caused the differences found in mean gut content, since the variation coefficient of a single plankton sample is known to be high (Cassie 1963). Larvae from the deepest layer had the lowest mean gut contents and the lowest percentage of feeders. It was concluded earlier that larvae without yolk sacs had higher mean gut contents than the others. The percentage of larvae at this stage was 18 in the deep layer as opposed to 53 in the two upper ones; therefore it is conceivable that the low mean gut content and low proportion of larvae feeding were due to the low percentage of larvae with absorbed yolk sacs found in this layer.

3. Defecation

Evidence for recent defecation was not found in this material. The high ratio of larvae with gut contents indicates that total defecation took place only to a lesser degree during capture and fixation.

Høglund (1968) observed a difference in the condition of the intestine between larvae that had apparently not contained any food for rather a long time and those that had emptied their guts shortly before capture. In the former the whole alimentary canal was transversely contracted with no hollowness visible, while in the latter the hindermost part of the gut immediately before the anus was more or less wide open. He also found a connection between time of feeding and ratio of larvae with distended guts. The condition of the intestine was recorded during the present investigation. After examination of larvae from the 25–5 m hauls no diurnal pattern could be seen in the ratio of larvae with distended guts. Eighty-eight per cent of 1371 larvae caught during daylight had distended guts, as had 90% of 625 larvae caught at night.

Some authors have observed partial or total defecation by stressed larvae (Hardy 1924, Blaxter 1965, Rosenthal and Hempel 1971). It is thus conceivable that larvae from hauls of short duration would contain more food than those from longer ones. The number of food particles from 108 larvae caught during daylight in the upper 25 m in six 5 minute hauls was compared with that of 235 larvae caught in 20 minute hauls immediately before or after the 5 minute hauls. No significant difference in number of food particles was found when applying a t-test. This does not indicate that no defecation occurred, it might just as well show that the degree of defecation at capture and fixation is the same in both types of hauls. However, the high ratio of larvae with gut contents (Fig. 1) indicates that total defecation only took place to a lesser degree during capture and fixation.

4. Selection of food particles. Food densities

The two dominant organisms in the zooplankton, *Calanus* eggs and nauplii, were also the two dominant food items. No correlation was found between the number of *Calanus* eggs in plankton and in guts.

Larvae consuming *Calanus* eggs had a less assorted diet than those eating *Calanus* nauplii.

When studying selection of food particles, only larvae caught together with the food, in this case only larvae from the daylight plankton hauls, should be examined. Unfortunately some of the plankton hauls had rather few herring larvae (Table 1). When the number of larvae from these hauls was less than 15, all larvae from the previous or following larval hauls were included. If the total number thus reached was still less than 15, the data were not used. A total of eight camparisons between plankton composition and gut contents could thus be made (Table 3). The ratio of *Calanus* eggs was usually higher in the larval guts than in plankton, while that of *Calanus* nauplii was lower, except when the density of nauplii exceeded ca. 5000 per m^3. Disregarding one observation, the percentage of *Microsetella* spp. and of other copepods was always higher in plankton than in the guts. Cyclopoid nauplii were not found in the guts of these larve although they constituted up to 25% of the plankton.

Blaxter (1965) stated that herring larvae 8 mm long could take food items up to 1.3 mm in length, and this would normally include stage II copepodites of *Calanus finmarchicus* (Wiborg 1948). This implies that most of the organisms present in plankton could have been ingested by the herring larvae (Table 3), but obviously *Calanus* eggs and nauplii were preferred.

Serveral authors report discrepancies between composition of gut contents of herring larvae and surrounding plankton. Hardy (1924) found that *Pseudocalanus* was preferred to *Acartia* even when both were present in equal numbers. Bhattacharyya (1957), on examining plankton from the same hauls as larvae, found that many more planktonic organisms were available

Table 3. Composition of zooplankton and gut contens of herring larvae caught concurrently.

Sample	4 April, 15 hrs.				5 April, 12 hrs.				5 April, 14 hrs.				6 April, 13 hrs.			
Depth interval	25–5 m				25–5 m				25–5 m				25–5 m			
No. of larvae from plankton hauls	17				27				35				9			
No. of larvae from larval hauls	0				0				0				32			
Food items	In plankton		In diet		In plankton		In diet		In plankton		In diet		In plankton		In diet	
	No./m³	%	No.	%	No./m³	%	No.	%	No./m³	%	No.	%	No./m³	%	No.	%
Calanus eggs	2 200	63.6	40	97.6	500	38.2	61	96.8	420	42.9	54	100	3 660	85.7	80	96.4
Calanus nauplii	300	9.5	0	0	60	4.6	0	0	110	11.2	0	0	340	8.0	2	2.4
Cyclopoid nauplii	450	13.0	0	0	330	25.0	0	0	20	2.0	0	0	90	2.1	0	0
Microsetella spp.	40	1.2	0	0	10	0.8	0	0	100	1.2	0	0	0	0	0	0
Other copepods	430	12.0	0	0	400	30,5	0	0	330	33.7	0	0	110	2.3	1	1.2
Other items	10	0.3	1	2.4	10	0.8	2	3.2	0	0	0	0	70	1.6	0	0

Continued:

Samples	4 April, 12 hrs.				6 April, 13 hrs.				7 April, 11 and 12 hrs.				9 April, 12 and 13 hrs.			
Depth interval	50–30 m				50–30 m				25–5 m				25–5 m			
No. of larvae from plankton hauls	15				30				1				2			
No. of larvae from larval hauls	0				0				24				27			
Food items	In plankton		In diet		In plankton		In diet		In plankton		In diet		In plankton		In diet	
	No./m³	%	No.	%	No./m³	%	No.	%	No./m³	%	No.	%	No./m³	%	No.	%
Calanus eggs	990	37.5	40	97.6	2 960	45.2	113	92.6	11 000	58.3	15	60.0	14 390	64.5	17	53.1
Calanus nauplii	550	20.3	0	0	2 680	40.9	6	4.9	5 320	28.2	8	32.0	5 240	23.5	11	34.4
Cyclopoid nauplii	620	23.9	0	0	150	2.3	0	0	350	1.9	0	0	260	1.2	0	0
Microsetella spp.	140	5.3	1	2.4	220	3.4	0	0	170	0.9	1	4.0	0	0	0	0
Other copepods	280	10.6	0	0	470	7.2	0	0	1 070	5.7	1	4.0	1 870	8.4	4	12.5
Other items	50	1.9	0	0	70	1.1	3	2.5	970	5.1	0	0	550	2.5	0	0

Table 4. Frequency of different kinds of gut content compared with yolk size. A χ^2 test for *k*-independent samples. E = Expected frequency. O = Observed frequency.

Gut Contents	Yolk sac size			Total
	Absorbed	Small	Medium and large	
Copepod eggs	E 281.8	807.5	88.6	
	O 276	820	82	1 178
Copepod eggs and other objects	E 33.5	96.0	10.5	
	O 35	89	16	140
Other objects	E 18.7	53.5	5.9	
	O 23	48	7	78
Total	334	957	105	1 396

$\chi^2 = 6.022$ df = 4 $p > 0.05$

than were eaten by the larvae. HENTSCHEL (1950) found that copepod nauplii were not eaten although they constituted up to 50% of the plankton, and that copepodites and adults were preferred instead although they constituted only 6%. WALDMANN (1961) found that copepods were by far preferred and the *Eurytemora* prevailed in the food in spite of its rare occurrence in the plankton.

A t-test for k independent samples (SIEGEL 1956) was applied to find out if a decrease in yolk sac size led to a change in the larval diet (Table 4). The test, comprising 1396 larvae containing food caught during daylight, did not show any significant change in composition of yolk sac size with different diets. Student t-tests on the same material did not reveal significant changes in mean length with different diets. This means that, within the size groups represented in this investigation, selection of food is not dependent on the age of the larva. This correlates with observations made by other authors (LEBOUR 1921, HARDY 1924, BOWERS and WILLIAMSON 1951) who found that changes in diet did not occur until after the yolk sac stage.

Table 3 shows a considerable increase in number of both *Calanus* eggs and nauplii on 7 and 9 April. In order to find any correlation between food items in the plankton and in the guts, the numbers of *Calanus* eggs and nauplii in plankton were rounded off to the nearest thousand and compared to the mean number of the same items per larva by the Spearman rank correlation coefficient (SIEGEL 1956) (Data from Table 3). Significant correlation was found with *Calanus* nauplii, but not with eggs.

To eliminate any possible influence of larvae too weak to feed, the mean numbers of eggs and nauplii per larva containing food were compared to the numbers of those items in the plankton. Again, significant correlation was found with nauplii, but not with eggs. Also the number of eggs and nauplii per larva containing food caught during daylight was correlated with the number of the same items in the plankton. The results were the same; significant correlation was found only between nauplii ingested and in plankton. A possible explanation for the above observations could be that the larvae had developed the habit of catching specific food items. After laboratory experiments Rosenthal (1969) suggested that herring larvae might gain preferece for certain kinds of food items during the early life stages, depending on their success in catching the first food particle. He also found that a change in diet from copepod nauplii to *Artemia* did not occur until 3-4 days after the other kind of food particle was added to the original ones. Thus the eight comparisons of diet and plankton composition in Table 3 might represent different larval populations, each population containing larvae searching for food items which they have been successful in catching previously. The increase in number of both eggs and nauplii on 7 and 9 April was obviously due to the fact that the floating drogue became surrounded by a different watermass. This increase in eggs would not lead to an increase in the number of eggs in the larval diet if the new watermass also contained larvae used to catching nauplii. This might also be the reason for the observed correlation between nauplii in plankton and diet. In the samples taken before 7 April the number of nauplii in plankton was low, and the larvae present were in the habit of catching eggs. The samples from 7 and 9 April had higher numbers of nauplii both in plankton and in the diet, and this made the correlation significant.

Of 1256 larvae containing *Calanus* eggs, 5% contained other food items; and of 40 larvae containing *Calanus* nauplii, 28% contained other food items. Larvae containing both eggs and nauplii are not included in these figures. Thus it seems that larvae eating nauplii have an increased ability to catch other food items compared to larvae eating eggs

Blaxter (1965) refers to investigations where food concentrations required by herring larvae varied from between 300 to 22 000 organisms/m^3. In the present investigation the densities of eggs added to nauplii varied from 530 to 18 990, with an average of 6 300 food praticles per m^3, *Calanus* eggs constituting 71% of these. However, since *Calanus* eggs constituted more than 90% of the gut contents and the nutritional value of one egg is low compared to that of the usually larger organisms reported to be eaten by herring larvae, the observed densities of food in the present work were probably still too low to maintain survival and growth. Also, the decrease in mean length of larvae without yolk sacs (Fig. 2) could indicate deficiency of suitable food after absorption of the yolk sac. Dragesund and

NAKKEN (1971) investigated mortality among larvae from the same larval patch as was studied in the present work. They found a reduction of about 95% of the larval population at a length which corresponded to the period of completion of yolk absorption.

THE CRITICAL PERIOD

The critical period concept suggested by HJORT (1914), maintains that the strength of a year-class is determined by the availability of planktonic food shortly after the larval yolk supply has been exhausted. MAY (1974) reviewed this concept in the light of ecological and experimental data. He stated that although other factors also undoubtedly influence larval survival at sea, field and laboratory data suggest that starvation may be an important cause of larval mortality at the end of the yolk sac stage.

Attempts have been made to compare the amount of gut contents of herring larvae with the abundance of available food. LISHEV, RANNAK and LISIVNENKO (1961) report a relationship between the abundance of herring and fry and the number of food organisms in the Bay of Riga from 1955 to 1961. (Quoted from BLAXTER and HOLLIDAY 1963). BAINBRIDGE and FORSYTH (1971) found high feeding intensities associated with high biomass of available prey organisms in the Clyde. SCHNACK (1972) found correlation between biomass in guts and in plankton. Several authors, however, report discrepancies between composition of gut contents and surrounding plankton. HARDY (1924) found that *Pseudocalanus* was preferred to *Acartia* even when present in equal numbers. BHATTACHARYYA (1957), on examining plankton from the same haul as the larvae, found that more planktonic organisms were available than were eaten by the fish. HENTSCHEL (1950) found that copepod nauplii were not eaten although they constituted up to 50% of the plankton, and that copepodites and adults were preferred instead, although they constituted only 6%. WALDMANN (1961) found that copepods were by far preferred and that *Eurytemora* prevailed in the food in spite of its rare occurrence in plankton. SCHNACK(1972) found it difficult to correlate the ingestion of copepod nauplii and gastropod larvae to their quantitative presence in plankton. LEBOUR (1924) found that herring larvae contained mainly molluscs, copepods and unicellular matter (green food remains). Disregarding the latter, as it is not clear whether this is eaten by the copepods before they themselves are ingested, her data shows that only 15% of the larvae containing molluscs and 14% of those containing copepods had other gut contents. DUKA(1968) characterised clupeoid larvae as stenophagous; i.e. the qualitative food components of the larvae are restricted to two or three species of organisms. This is probably the explanation of the findings mentioned previously. The different larval populations become accustomed to catching certain food items and continue to search for these despite greater abundance of other food organisms.

Herring larvae are known to start feeding while they still have large yolk sacs, most probably in order to be able to catch food items when the yolk sac is eventually absorbed and they become dependent on external food.

As food objects *Calanus* eggs are non-motile and without spines, and should thus be easy to catch from any direction. However, they hatch within 24 hours, while development through the nauplius stages lasts for at least 20 days (JONES and HALL 1974). Even if single *Calanus* females are observed to spawn over several weeks (MARSHALL and ORR 1955) and eggs are thus to be found over a long period, nauplii are available over a much longer period. So, if a larva gains preference for *Calanus* eggs because of a temporarily high percentage in the plankton, it will still be searching for them when it becomes dependent on external food. At this stage the surrounding food items might consist mainly of nauplii hatched from the eggs. ROSENTHAL (1969) found that herring larvae needed 3–4 days to change from ingesting copepod nauplii to taking *Artemia*, in other words, from one motile organism to another. The time needed to change from non-motile *Calanus* eggs to nauplii as diet might be longer and thus exceed the time required to reach the «point of no return» as indicated by BLAXTER and EHRLICH (1974). This describes the point at which 50% of a larval population are too weak to feed if food becomes available. For herring larvae this was found to occur six days after absorption of the yolk sac. Difficulties in changing from non-motile to motile food items may also account for the rather low percentage of larvae observed containing *Calanus* eggs together with other food items in this investigation.

On the other hand, larvae starting to feed in a watermass where *Calanus* nauplii are the dominant food items have a lesser likelihood of entering watermasses containing unfamiliar food organisms, as nauplii are present in plankton for a much longer period than eggs and are thus more dispersed. It also seems from the present investigation that the ability to catch nauplii increases the ability to catch other motile food items, since the percentage of larvae containing both nauplii and other food organisms was rather high. This could increase the chance for survival due to the wider food range available to the larvae.

DRAGESUND (1970) stressed the importance of coincidence in time between hatching of herring larvae and the occurrence of suitable food when considering the survival of the larvae. It appears that this coincidence must be emphasized; not only must suitable food be present when the larvae start to feed, but if they gain preference for certain kinds of food at this stage, as suggested by ROSENTHAL (1969), it is of importance for the survival that the same kind of food is available and abundant when they become dependent on external food. This implies that larvae starting to feed when *Calanus* eggs are predominant in plankton have less chance of surviving than those starting to feed when nauplii are abundant.

CONCLUSION

The kind of food particles eaten by smaller larvae of Norwegian spring spawners was similar to that of herring larvae of other races. The proportion of copepod eggs in the diet however, was different, constituting more than 90% of the food items.

Feeding seemed to start shortly after sunrise within the same hour in the depth intervals 25–5 m, 30–50 m and 75–55 m.

The length range of larvae with different yolk sac sizes overlapped considerably, yet t-tests showed an increase in mean length with decreasing yolk sac size, except for larvae with absorbed yolk sacs which were shorter than those with small yolk sacs. This could indicate lack of suitable food after the yolk sac stage.

The percentage of larvae feeding increased with decreasing yolk sac size, but the mean gut content of feeding larvae did not increase until after absorption.

Larvae from the deepest strata, 75–55 m, had less gut contents than the others, probably because of a lower percentage of larvae with absorbed yolk sacs in this depth layer.

Some authors report larvae defecating partially or totally when stressed. Larvae from hauls of short duration did not have greater gut contents than larvae from longer ones. Total defecation was contradicted by the high ratio of feeding larvae caught during daylight.

No correlation was found between the number of *Calanus* eggs in the guts and in plankton. Larvae containing nauplii had more assorted gut contents than larvae containing eggs.

A «critical period» could arise when larvae having learned to feed on *Calanus* eggs have to change to motile objects when nauplii hatch.

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ANALYSIS OF EMPIRICAL OBSERVATIONS ON THE SCATTERING OF SOUND BY ENCAGED AGGREGATIONS OF FISH

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ABSTRACT

FOOTE, K. G. 1978. Analysis of empirical observations on the scattering of sound by encaged aggregations of fish. *FiskDir. Skr. Ser. HavUnders.*, *16*: 422–455.

The experimental findings of RØTTINGEN (1975 and 1976) for the scattering of ultrasonic sound by encaged aggregations of saithe and sprat are analyzed. The insensitivity of the relationship of the mean time-integrated echo intensity $\bar{\varepsilon}$ and fish number density ν to both the center frequency and pulse duration of the ensonifying signal is considered qualitatively. A general theory for the scattering of sound by a collection of randomly distributed and oriented, but otherwise identical scatterers, whose individually complicated scattering behavior is described by two parameters, the backscattering and extinction cross sections, is applied to Røttingen's experiment with saithe. The empirical ε–ν relationship is reproduced successfully with respect to a unique set of parameters of a model whose main ingredients are the following: assumption of a truncated Gaussian distribution in tilt angle for the orientation distribution; expression of the scattering cross sections in terms of the mean and variance of this distribution; assumption that the mean tilt angle is independent of ν and that the variance in tilt is the sum of two variances: the intrinsic variance, which is postulated to be an exponentially decreasing function of ν, and the perspectival variance, assumed constant, which is the mean square apparent tilt of the scatterer due solely to its azimuthal orientation relative to the generally obliquely located source/receiver. By comparing predictions of the $\bar{\varepsilon}$–ν relationship with those observed for saithe, the mean extinction cross sections at the two frequencies of Røttingen's experiment are deduced.

INTRODUCTION

In an experiment performed by Røttingen in 1973 (RØTTINGEN 1975 and 1976), which was designed to help clarify the relationship between acoustic echo energy and the number density of schooling fish when ensonified by ultrasonic pulses, the echoes from encaged aggregations of fish of uniform kind and size were observed. By elementary signal processing the information contained in each echo was reduced to a single number, the time-

integrated echo intensity ε. Because of the considerable pulse-to-pulse variability in this quantity, many determinations of ε were made at each observed number density ν. A large number of independent samples were then drawn from this population of measurements and their average, $\bar{\varepsilon}$, computed with respect to this ensemble, so that the true $\bar{\varepsilon}$ at a particular number density would be known with a high degree of confidence. This determination of $\bar{\varepsilon}$ was made systematically over a wide range of ν, which probably spans that observed in nature, for each of three species of fish: *Pollachius virens* (L.) or saithe, *Sprattus sprattus* (L.) or sprat, and *Scomber scombrus* L. or mackerel.

The surprising finding of the observations on the saithe and sprat was that the relationship of $\bar{\varepsilon}$ and ν is essentially non-unique, and is distinguished primarily by fish kind and size and only secondarily by pulse duration and center frequency. The basic ν-dependence of $\bar{\varepsilon}$ is the following: linear proportionality up to a certain density; thereafter, a steady decrease in the rate of increase of $\bar{\varepsilon}$ with ν until a maximum is reached; then, a decline in $\bar{\varepsilon}$ for still higher values of ν. Thus there are values of $\bar{\varepsilon}$ which obtain at each of two distinct densities.

The observations of $\bar{\varepsilon}$ for the mackerel were quite irregular. Because these fish were observed, by mean of an underwater camera, to cluster along the netting of their cage, rather than to distribute themselves more or less uniformly throughout it as both the saithe and sprat did, their observations are not considered further in this study.

It is the aim this paper, then, to explain the basic observations of Røttingen for saithe and sprat. This will be done firstly on a qualitative level: the approximate insensitivity of the $\bar{\varepsilon}$–ν relationship to the pulse duration and center frequency of the ensonifying signal will be explained and, through a dimensional analysis of the empirical findings, the requirements for a quantitative theory will be established. A general theory for the scattering of sound by collections of scatterers, which is developed in the Appendix, will then be applied to Røttingen's experiment with saithe. A similar detailed quantitative analysis for sprat will not be carried out because of the lack of ventral aspect target strength data for sprat, which will be seen to be of crucial importance in the determination of the precise form of the $\bar{\varepsilon}$–ν relationship.

METHOD

QUALITATIVE ANALYSIS OF RØTTINGEN'S OBSERVATIONS

For convenience Røttingen's results are reproduced in a condensed format in Fig. 1 and 2. In both figures, which are distinguished by fish species and size, the empirical relationship of the mean or ensemble-averaged time – integrated echo intensity $\bar{\varepsilon}$ and fish number density ν is

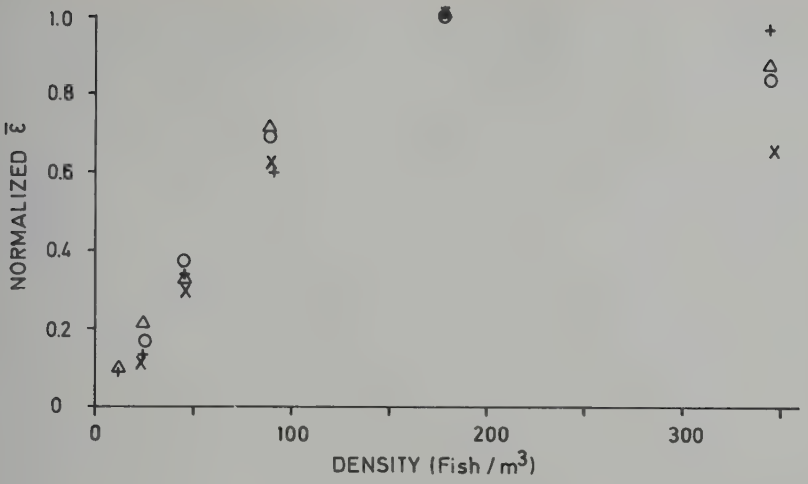

Fig. 1. Røttingen's observations of the normalized mean time-integrated echo intensity $\bar{\varepsilon}$ for saithe when ensonified by a narrowband signal for four conditions of pulse duration and center frequency: 0.3 msec at 38 kHz (o), 0.6 msec at 38 kHz (△), 0.1 msec at 120 kHz (+), and 0.6 msec at 120 kHz (x).

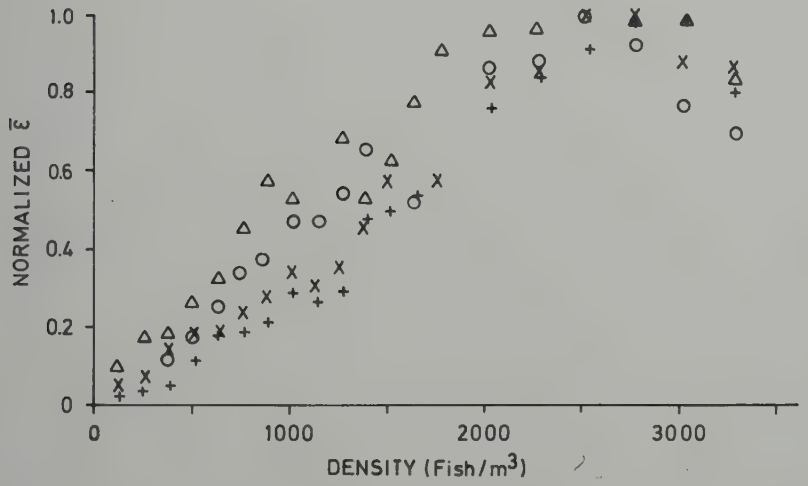

Fig. 2. Røttingen's observations of the normalized mean time-integrated echo intensity $\bar{\varepsilon}$ for sprat when ensonified by a narrowband signal for the same four conditions of pulse duration and center frequency shown in the legend of Fig. 1.

stated for the following four combinations of pulse duration T and center frequency $\omega_o/2\pi$ of the ensonifying signal: $T = 0.3$ and 0.6 msec for $\omega_o/2\pi =$ 38 kHz and $T = 0.1$ and 0.6 msec for $\omega_o/2\pi = 120$ kHz; all for a pulsed sinusoid of the form $\text{rect}(t/T)\cos(\omega_o t)$, as expressed in the notation of WOODWARD (1964). The four empirical $\bar{\varepsilon}$–ν relationships are stated for saithe of uniform length distribution 35.1 ± 0.6 cm and mean mass 375 g in Fig. 1 and for sprat of uniform length distribution 12.1 ± 2.3 cm and mean mass 12 g in Fig. 2.

In view of the wide ranges in center frequency and pulse duration represented by the data, it is concluded that the $\bar{\varepsilon}$–ν relationship is generally insensitive to both center frequency and pulse duration of the ensonifying signal, at least for the narrowband pulsed sinusoidal type, and is distinguished primarily by fish kind and size.

That the $\bar{\varepsilon}$-ν relationship is relatively insensitive to frequency is not difficult to explain. This is because all estimates of a characteristic scattering size a indicate that the characteristic size-to-wavelength ratio is such that the proportional quantity $ka = 2\pi a/\lambda$, where k is the wavenumber and λ is the wavelength of the signal at its center frequency, is always in excess of unity and generally is much greater than unity. Such estimates of the characteristic scattering size include those deduced from the following three sources: (1) the gross dimensions of the fish (RØTTINGEN 1976, RASMUSSEN 1960, NAKKEN pers. com.); (2) the size of the swimbladder, the chief scattering organ of these species of fish, based on the estimate that the swimbladder occupies roughly 5 per cent of the total volume (SHIBATA 1970, MCCARTNEY and STUBBS 1971); and (3) measurements of target strength, assuming approximate equality of peak ventral and dorsal aspect target strengths (NAKKEN and OLSEN 1973). In the limit that the size is much larger than the wavelength, the phenomenon of scattering is essentially geometric, and those quantities which describe the scattering behaviour of a body, for example, a fish, adopt their respective constant high frequency values. Thus, other things remaining unchanged, a change in magnitude of the center frequency of the ensonifying signal, if sufficiently high, say, above 38 kHz, should not affect the relationship of $\bar{\varepsilon}$ and ν.

The relative insentitivity of the $\bar{\varepsilon}$–ν relationship to changes in pulse duration can also be understood rather simply. The photographic evidence of Røttingen's experiment showed the spatial distribution of fish in their net cage to be generally randomly homogeneous throughout the entire volume of the cage. The pulse-to-pulse variations in the time-integrated echo intensity were large, suggesting both the importance of coherence for particular ε and the fact that the fish did not remain stationary, but moved about. That this internal movement provides a mechanism for the randomness of ε is clear, for while the ensonifying signal was narrowband, with $\omega_o T >> 1$ for all experimental conditions of ω_o and T, the fish densities were always such

that the mean nearest-neighbour fish distance was much greater than the wavelength, i.e. $v^{-1/3} \gg \lambda$. Thus the phases or relative times of the constituent echoes from individual fish, which compose the whole echo, are entirely random. The effect of this is to cause the coherent contribution to ε to vanish in the mean of large numbers of independent observations of ε at particular ν, so that $\bar{\varepsilon}$ is equal to the irreducible incoherent contribution alone. This non-vanishing component of $\bar{\varepsilon}$ is linearly proportional to T as the energy contained in each constituent echo is exactly proportional to the energy contained in the ensonifying signal, which for the pulsed sinusoids of Røttingen's experiments is proportional to T. The basic form of the $\bar{\varepsilon}$–ν relationship, when normalized by or scaled to the maximum value of $\bar{\varepsilon}$ for the particular experimental conditions of ω_o and T, should, therefore, be independent of the pulse duration T.

The implication of the insensitivity of the $\bar{\varepsilon}$–ν relationship to ω_o and T for both the saithe and sprat of Røttingen's experiments is that the phenomenon of echo formation by an encaged aggregation of fish at ultrasonic frequencies is primarily geometric and incoherent. The principal evidence for this conclusion is that a variation in frequency by a factor of three and a variation in pulse duration, thence phase, by a factor of six, with corresponding changes in the scatterer size-to-wavelength ratio and mean scatterer separation-to-pulse length ratio, have only an indiscernible effect on the ν-dependence of $\bar{\varepsilon}$. If the mean echo strength were very dependent on the coherent or physical effect of interference among the constituent echoes, then there almost certainly would be considerable variations in the $\bar{\varepsilon}$–ν relationship as T and ω_o were varied; yet, what variations are present are slight and apparently even too inconsistent to justify speculation about their origin. The fact that the $\bar{\varepsilon}$–ν relationship is stable with respect to large changes in both T and ω_o for different kinds of fish of uniform size distributions, but of widely differing mean lengths and masses, strengthens the conviction that a purely geometric theory of scattering should be entirely adequate to explain the quantitative features of the $\bar{\varepsilon}$–ν relationship.

Such a theory, which is developed in the Appendix and which has some common features with the theory of acoustic scattering by wakes (Wildt 1947), is applied to the problem of Røttingen's experiment with saithe in the next section.

QUANTITATIVE ANALYSIS OF RØTTINGEN'S OBSERVATIONS

I Scattering of sound by an aggregation of fish

The theory for acoustic scattering by a collection of randomly distributed and oriented, but otherwise identical scatterers, which is presented in

the Appendix, can be applied to the problem of acoustic scattering by an aggregation of fish if the following assumptions are made:

(1) the acoustic source and receiver are essentially collocated;
(2) the ensonifying signal is narrowband and of such a center frequency that the only significant multiple scattering effect is that of extinction of the incident wave;
(3) the amplitude of the signal is sufficiently weak so that all nonlinear effects can be ignored;
(4) the fish distribute themselves randomly homogenously throughout a definite volume which is fixed relative to the source/receiver and in the farfield of the source/receiver;
(5) the fish are identical in size;
(6) the scattering parameters of a single fish can be represented by exactly two parameters, the backscattering and extinction cross sections, which generally are functions of the orientation of the fish.

When these conditions are satisfied, according to the results of the Appendix, the mean or ensemble-averaged time-integrated echo intensity $\bar{\varepsilon}$ can be written

$$\bar{\varepsilon} = \frac{I_o \varrho(0)}{4\pi} \sum_n \frac{D_{S,n}^2 D_{R,n}^2}{r_n^4} \sigma_{b,n} \exp[-4\alpha r_n - \nu \bar{\sigma}_e (r_n - r_{n,o})]$$

where the overhead bar denotes the operation of ensemble-averaging, and where the several quantities have the following meanings

I_o is the peak instantaneous intensity of the ensonifying pressure field at unit distance from the source;
$\varrho(0)$ is the maximum value of the signal autocorrelation function;
$\sigma_{b,n}$ is the backscattering cross section of the n^{th} scatterer;
$D_{S,n}$ and $D_{R,n}$ are the respective source and receiver pressure directivity factors in the direction of the n^{th} scatterer;
r_n is the distance between source and n^{th} scatterer;
α is the attenuation rate of the medium at the center frequency of the ensonifying signal;
ν is the scatterer or fish number density;
$\bar{\sigma}_e$ is the ensemble-averaged extinction cross section;
$r_{n,o}$ is the distance from source to nearest surface of the volume in the direction of the n^{th} scatterer.

II. Approximation of $\bar{\varepsilon}$ for a particular geometry and its evaluation for constant scattering parameters.

In order to gain some insight into the above expression for $\bar{\varepsilon}$, which, under certain circumstances, could represent the mean acoustic energy backscattered by an aggregation or school of fish, $\bar{\varepsilon}$ is now examined for a particular geometry. For convenience this is chosen to be of the type used by Røttingen in his experiments.

Consider a cylindrical volume V boulding a collection of scatterers which are distributed randomly, but homogeneously throughout it. V is aligned with the common principal response axis of essentially collocated source and receiver. The position of the source/receiver defines the origin of a coordinate system whose z-axis is that of the common principal response axis. The transmit and receive beam patterns are broad with respect to V, which, further, is assumed to be sufficiently narrow so that the contribution to the echo from a single scatterer is, to a good approximation, independent of its location in any transverse plane of V. The general expression for $\bar{\varepsilon}$ can be reduced to the following:

$$\bar{\varepsilon} = \frac{I_o \varrho(0) V}{4\pi (z_2 - z_1)} \nu \bar{\sigma}_b \int_{z_1}^{z_2} \frac{exp\,[-4\alpha z - \nu \bar{\sigma}_e (z - z_1)]}{z^4}\, dz$$

where z_1 and z_2 are the distances from source to nearer and further bounding planes of V, respectively, and where V is the measure of the cylindrical volume.

The integral in this expression for $\bar{\varepsilon}$ can be reduced to the exponential integral, so that $\bar{\varepsilon}$ can be expressed in the following alternative form:

$$\bar{\varepsilon} = \frac{I_o \varrho(0) V}{24\pi l} \nu \bar{\sigma}_b \; exp(-4\alpha z_1)\, Y(4\alpha + \nu \bar{\sigma}_e)$$

where $l = z_2 - z_1$ and

$$Y(a) = \int_{z_1}^{z_2} \frac{exp\,[-a(z - z_1)]}{z^4}\, dz = 2\left[\frac{1}{z_1^3} - \frac{exp\,(-al)}{z_2^3}\right] - a\left[\frac{1}{z_1^2} - \frac{exp\,(-al)}{z_2^2}\right]$$

$$+ a^2\left[\frac{1}{z_1} - \frac{exp\,(-al)}{z_2}\right] - \alpha^3\, exp(\alpha z_1)\left[E_1(a z_1) - E_1(a z_2)\right]$$

where $E_1(x)$ is the exponential integral

$$E_1(x) = \int_x^\infty \frac{exp\,(-t)}{t}\, dt$$

as defined in Abramowitz and Stegun (1964).

If the ensemble-averaged scattering cross sections $\bar{\sigma}_b$ and $\bar{\sigma}_e$ are regarded as constants, independent of the scatterer number density ν, then inspection of the integral expression of $\bar{\varepsilon}$ shows that $\overline{\varepsilon(\nu)}$ is a monotonically increasing function of ν, which increases linearly with ν for small ν and gradually becomes asymptotic to a constant for large ν. These limiting forms of $\bar{\varepsilon}$ are the following:

$$\overline{\varepsilon(\nu)} \underset{\nu \to 0}{\sim} c(c_1\nu - c_2\nu^2) + 0(\nu^3)$$

$$\overline{\varepsilon(\nu)} \underset{\nu \to \infty}{\sim} c_3 - \frac{c_4}{\nu} + 0\left(\frac{1}{\nu^2}\right)$$

where

$$c = \frac{I_o \varrho(0) V \bar{\sigma}_b}{4\pi l}$$

$$c_1 = \int_{z_1}^{z_2} \frac{exp\ (-4\alpha z)}{z^4}\, dz$$

$$c_2 = \bar{\sigma}_e \left[\int_{z_1}^{z_2} \frac{exp\ (-4\ \alpha z)}{z^3}\, dz - z_1 c_1 \right]$$

$$c_3 = \frac{c\ exp\ (-4\alpha z_1)}{\bar{\sigma}_e\, z^4}$$

$$c_4 = \frac{4c_3}{\bar{\sigma}_e} (\alpha + \frac{1}{z_1})$$

These limiting forms of $\overline{\varepsilon(\nu)}$ confirm what is expected from simple physical considerations. In the limit of very low densities the several echoes from individual scatterers are generally distinct, i.e., separated in time, since a density can be found for which the signal transmission time T is relatively short compared to the mean time difference between the echoes of nearest-neighbour scatterers, so that the total echo energy is merely the sum of the individual echo energies; thence, $\bar{\varepsilon}$ is proportional to the number of scatterers in V, and thence to ν. At high densities the effect of extinction is strong; in fact, the diminution of the incident acoustic field as it penetrates V exactly counterbalances the increased number of scatterers, whose mean

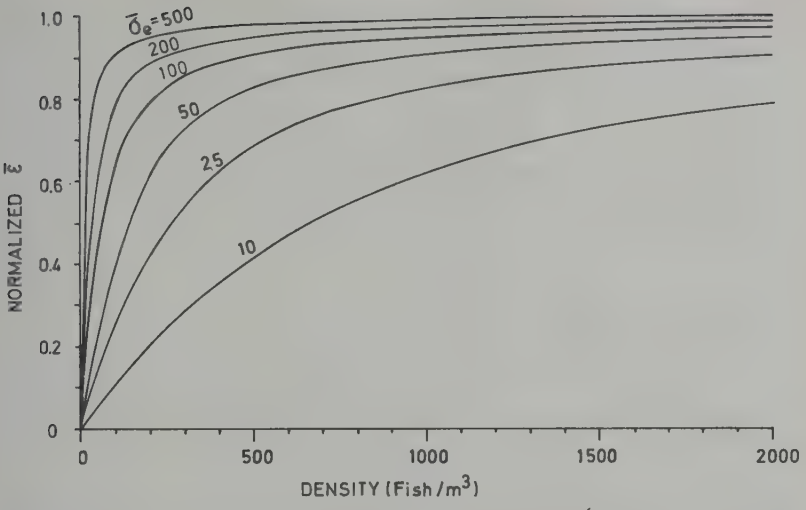

Fig. 3. Normalized mean time-integrated echo intensity $\bar{\varepsilon}$ for a collection of scatterers with constant $\bar{\sigma}_b$ and $\bar{\sigma}_e$ when ensonified by a narrowband signal of center frequency 38 kHz. $\bar{\sigma}_e$ is expressed in units of sqvare centimeters.

contribution to the irreducible incoherent part of $\bar{\varepsilon}$ is inversely proportional to the total number νV of scatterers, and thence to ν, so that $\bar{\varepsilon}$ steadily approaches a constant as ν increases. This asymptotic behaviour is a manifestation of conservation of energy: only a finite amount of energy is contained in $s(t)$ and only a finite amount of energy – at most, that which is intercepted by V – can be backscattered. If, moreover, at all values of ν the scatterers are distributed randomly homogeneously in V, so that $\bar{\varepsilon}$ is composed only of its incoherent part, then the transition from linear growth at low densities to asymptotic constancy at high densities will be completely smooth and gradual, i.e., monotonic.

If a scatterer is of finite size and simple shape, then in the limit of the highest densities the distribution of scatterers in V may become regular, in which case the interference of the constituent echoes will make a non-negligible contribution to the total echo. The amount of acoustic energy intercepted and backscattered by V is still finite in this situation, but the dependence of $\bar{\varepsilon}$ on the now significant coherent part of the echo, in addition to the irreducible incoherent part, renders the asymptotic approach to a constant at the highest density non-monotonic, or oscillatory, in the general case. The precise approach to the high density asymptote depends on the precise narrowband signal, scatterer size, geometry of V and magnitude of $\bar{\sigma}_e$ for the case of constant, density-independent $\bar{\sigma}_b$ and $\bar{\sigma}_e$.

As an illustration of the dependence of $\bar{\varepsilon}$ on ν for constant $\bar{\sigma}_b$ and $\bar{\sigma}_e$, the results of a calculation of $\bar{\varepsilon}$ for the case of a 38 kHz narrowband signal and cylindrical volume with $z_1 = 7.7$ m and $z_2 = 9.5$ are presented in Fig. 3. These results are shown for a range of values of the constant extinction cross section $\bar{\sigma}_e$ and are normalized to their respective high density asympotic values. Comparable results for the case of a 120 kHz narrowband signal are nearly indistinguishable from these and are, therefore, omitted.

III. *Application of theory to Røttingen's experiment with saithe.*

The particular geometry that was chosen for the approximation of the general expression for the ensemble-averaged time- integrated echo intensity in the preceding section is similar to that used by Røttingen in his experiments. For the measurements on saithe, the fish were contained in an approximately cylindrical net cage of height 180 cm and radius which varied smoothly between 70 cm and 72.5 cm. The cage was oriented vertically with its longitudinal axis nearly coincident with the common transmitting/receiving axes of acoustic transducers at 38 and 120 kHz, each of which was used in its dual transmitting/receiving capacity. The transducers were placed below the cage, which was located near the surface to facilitate the transfer of fish, so that the saithe were ensonified ventrally, instead of dorsally as is customany in such work. The distances from the transducers to the nearer and further bounding planes of the cylindriform net cage were 7.7 m and 9.5 m, respectively. The configuration of transducers and cage were such that the maximum degradation in sound source level over the cage, because of transducer directivity, in the worst case was less than 1.5 dB. All photographic observations of the saithe showed that they were distributed more or less uniformily throughout the volume and adopted no particular orientation or attitude as they might be expected to do when schooling, for example.

The circumstances of Røttingen's experiment evidently fulfill the conditions under which the general expression for $\bar{\varepsilon}$ was reduced to the simple one-dimensional integral approximation earlier, if the slight variation in sound level due to transducer directivity over the net cage is ignored, with a single difference: that the scattering properties of the saithe must be evaluated for the ventral aspect rather than the dorsal aspect. The applicability of the approximation to $\bar{\varepsilon}$ for Røttingen's experiment is thus established; evaluation of it, if satisfactory, should disclose the mechanisms underlying the observations shown in Fig. 1 and, presumably, by analogy, those for the sprat which are shown in Fig. 2.

That Røttingen's observations cannot be explained by a model in which the scattering parameters $\bar{\sigma}_b$ and $\bar{\sigma}_e$ are both independent of the fish num-

ber density ν is clear. Such a model can explain only a monotonic increase in $\bar{\varepsilon}$ with ν which becomes asymptotic to a constant at very high densities, as is illustrated in Fig. 3. The scattering parameters $\bar{\sigma}_b$ and $\bar{\sigma}_e$ must, therefore, depend on ν.

It is not surprising that $\bar{\sigma}_b$ and $\bar{\sigma}_e$ should depend on ν when it is considered that as the number, thence density, of fish in the net cage increases, an individual specimen has less space in which to move and, consequently, must curtail its orientation range to avoid interfering with its neighbours, which would be individually and socially harmful, thence prohibited. Thus, the ensemble-averages of σ_b and σ_e, which generally vary with the orientation of the scatterer, or fish, relative to the direction of ensonification, will depend on ν. In the absence of any quantitative information about the aggregating properties of the encaged saithe of Røttingen's experiment, or, in fact, of the encaged fish of any other study, a rather simple, but plausible model for the orientation distribution of the encaged saithe is proposed. A model which connects the spread of this distribution with the fish number density ν is also proposed so that $\bar{\sigma}_b$ and $\bar{\sigma}_e$, which are expressed in terms of the characteristic measures of the orientation distribution, can be computed directly in terms of ν.

In the course of determining the density-dependence of $\bar{\varepsilon}$ for the particular conditions that obtained during Røttingen's experiments with saithe, which is contained in the factor

$$\nu\bar{\sigma}_b \int_{z_1}^{z_2} \frac{exp\ [-4\alpha z - \nu\bar{\sigma}_e(z-z_1)]}{z^4}\, dz$$

where $z_1 = 7.7$ m, $z_2 = 9.5$ m and a is the medium attenuation rate at either 38 kHz or 120 kHz; an orientation distribution for the saithe is proposed; $\bar{\sigma}_b$ and $\bar{\sigma}_e$ are evaluated in terms of the variance and mean of this distribution; and the variance of this distribution is expressed as a function of the fish number density ν, so that the expressions for $\bar{\sigma}_b$ and $\bar{\sigma}_e$ can be evaluated directly in terms of ν.

IIIa. *Orientation distribution.*

The form of the orientation distribution that obtained during Røttingen's experiment with the saithe is unknown; it was not measured, and there is no formal theory which specifies the orientation distribution of encaged aggregations of saithe or of any other kind of fish. But insofar as the fish were observed to adopt a more or less random distribution in inclination about a horizontal or near-horizontal inclination, and insofar as saithe has a

dorsal aspect target strength which is rater insensitive to roll over a 60 degree range (NAKKEN and OLSEN 1973), there appears to be plausibility to the selection of a very simple form for this distribution, as is explained below.

The swimbladder, when present in fish as it is in a well-developed state in saithe, is recognized – see, for example, SHIBATA (1970), HARDEN JONES and PEARCE (1958) and CUSHING and RICHARDSON (1955) – to contribute significantly to the echo, even at ultrasonic frequencies. The fact that this organ is approximately cylindriform and generally is more or less aligned with the fish center line, which is defined here as the line running from the front of the upper jaw to the root of the tail, suggests that the principal scattering properties of the fish, and not merely its echo, are rather insentitive to roll, at least over that angular range where the swimbladder presents a similar surface. This has been confirmed by measurements of the dorsal aspect target strength of saithe, cod and herring (NAKKEN and OLSEN 1973). Inspection of the morphology of saithe (ROLLEFSEN 1960–62 and MIDTTUN and HOFF 1962) suggests that the ventral aspect target strength and, presumably, other similar primary scattering characteristics are insensitive to roll. It may be inferred, therefore, that the dependence of the orientation distribution of saithe on roll may be ignored since the scattering properties of interest, σ_b and σ_e, and their ensemble averages will be similarly insensitive with respect to roll.

Since the saithe of Røttingen's experiment were observed to adopt a more or less random distribution in inclination about some approximately horizontal mean inclination, the orientation distribution may plausibly be described by a truncated Gaussian distribution in inclination or tilt angle θ, which is defined as the angle that the center line of the fish makes with the horizontal plane. This distribution is described by the probability density function

$$f(\theta) = \begin{cases} \dfrac{1}{\sqrt{2\pi}\,\sigma_\theta} \exp\left[-\dfrac{(\theta-\bar{\theta})^2}{2\sigma_\theta^2}\right] & \text{for } |\theta-\bar{\theta}| \leqq \lambda'\sigma_\theta \\ 0 & \text{for } |\theta-\bar{\theta}| > \lambda'\sigma_\theta \end{cases}$$

were λ' is a factor of the order of three if the results of OLSEN (1971) for cod in the open sea are applicable. The normalizing factor $1/\sqrt{2\pi}\sigma_\theta$ is rigorously true only for infinite λ', but is underestimated by .3% for $\lambda'=3$, 1.3% for $\lambda'=2.5$ and 4.6% for $\lambda'=2$. The mean angle of inclination $\bar{\theta}$ may be assumed to be small and constant with respect to the density ν of fish, and the standard deviation σ_θ of the distribution is presumed to be a monotonically decreasing function of ν. The precise dependence of σ_θ on ν is discus-

sed below, after the ensemble averages of σ_b and σ_e have been expressed as functions of σ_θ and $\bar{\theta}$, the characterizing parameters of the orientation distribution.

IIIb *Ensemble-averaged backscattering cross section.*

As the spatial distribution of the saithe in Røttingen's experiment was observed to be approximately randomly homogeneous throughout the net cage, the ensemble average of a scattering parameter such as σ_b or σ_e is just the average of the same quantity with respect to the orientation distribution, which, by the discussion of the previous section, is assumed to be described adequately by the probability density function $f(\theta)$. Thus, the average of the backscattering cross section σ_b with respect to the ensemble of naturally occuring configurations at a given fish number density ν, and thence at a fixed distribution spread σ_θ, is

$$\bar{\sigma}_b = \int \sigma_b(\theta) f(\theta) d\theta$$

where the range of integration is $[\bar{\theta} - \lambda' \sigma_\theta, \bar{\theta} + \lambda' \sigma_\theta]$.

The backscattering cross section is known through the more commonly measured target strength function $TS(\theta)$, which is related to $\sigma_b(\theta)$ by the usual definition (URICK 1975):

$$TS(\theta) = 10 \log_{10} \frac{\sigma_b(\theta)}{4\pi}$$

so that $\bar{\sigma}_b$ may be computed directly in terms of $TS(\theta)$ by the formula

$$\bar{\sigma}_b = 4\pi \int 10^{TS(\theta)/10} f(\theta) d\theta$$

It was this expression of $\bar{\sigma}_b$ that was evaluated for the particular conditions of Røttingen's experiment with saithe, which are expressed here through the two target strength functions shown in Fig. 4. These functions are distinguished by the center frequency of the ensonifying pulse, which was 38 kHz in one instance and 120 kHz in the other. Both curves represent averages of measurements of the ventral aspect target strength function with respect to a number of specimens of saithe actually used in the experiment. In particular, the target strength function at 38 kHz is the result of averaging the target strength functions of 16 specimens, while that at 120 kHz is the result of averaging the target strength functions of 17 specimens.

The result of evaluating $\bar{\sigma}_b$ numberically for the case that $\lambda' = 3$ is shown

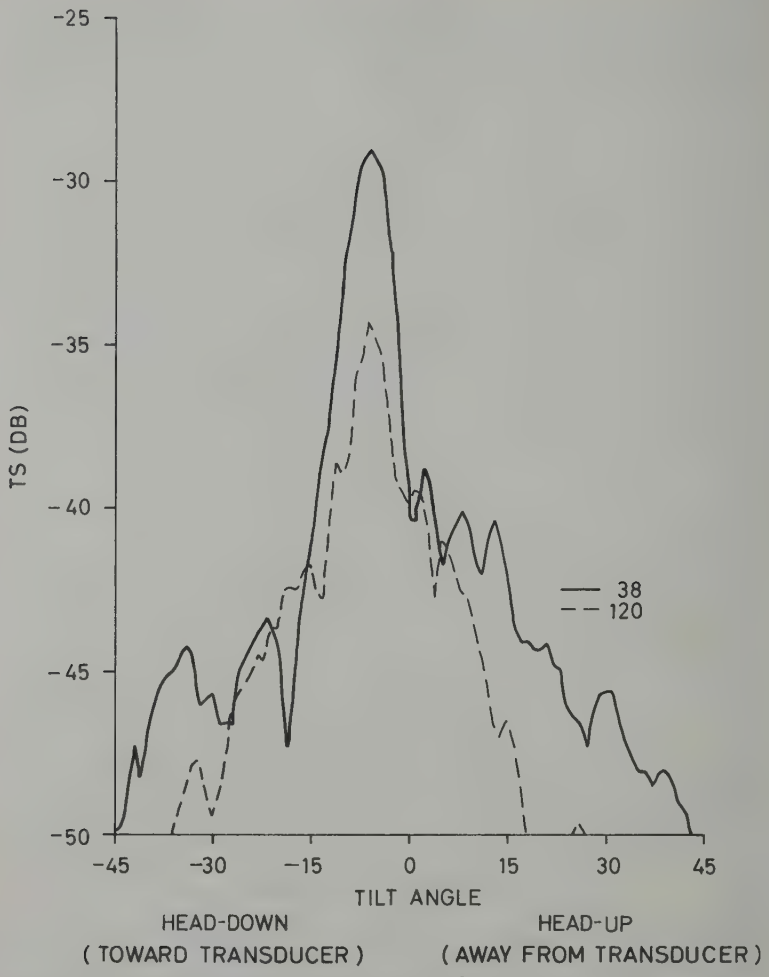

Fig. 4. Ventral aspect target strength of saithe of mean length 35.1 ± 0.6 cm at 38 kHz when averaged with respect to 16 specimens, and at 120 kHz when averaged with respect to 17 specimens.

in Fig. 5 and 6, which apply to the respective narrowband ensonifying signals with center frequencies of 38 kHz and 120 kHz. Because the mean and unknown tilt angle $\bar{\theta}$ is presumed constant with respect to the fish number density ν, while σ_θ is presumed to vary systematically with ν, $\bar{\sigma}_b$ is shown as a function of σ_θ, with $\bar{\theta}$ as a parameter which is varied over the

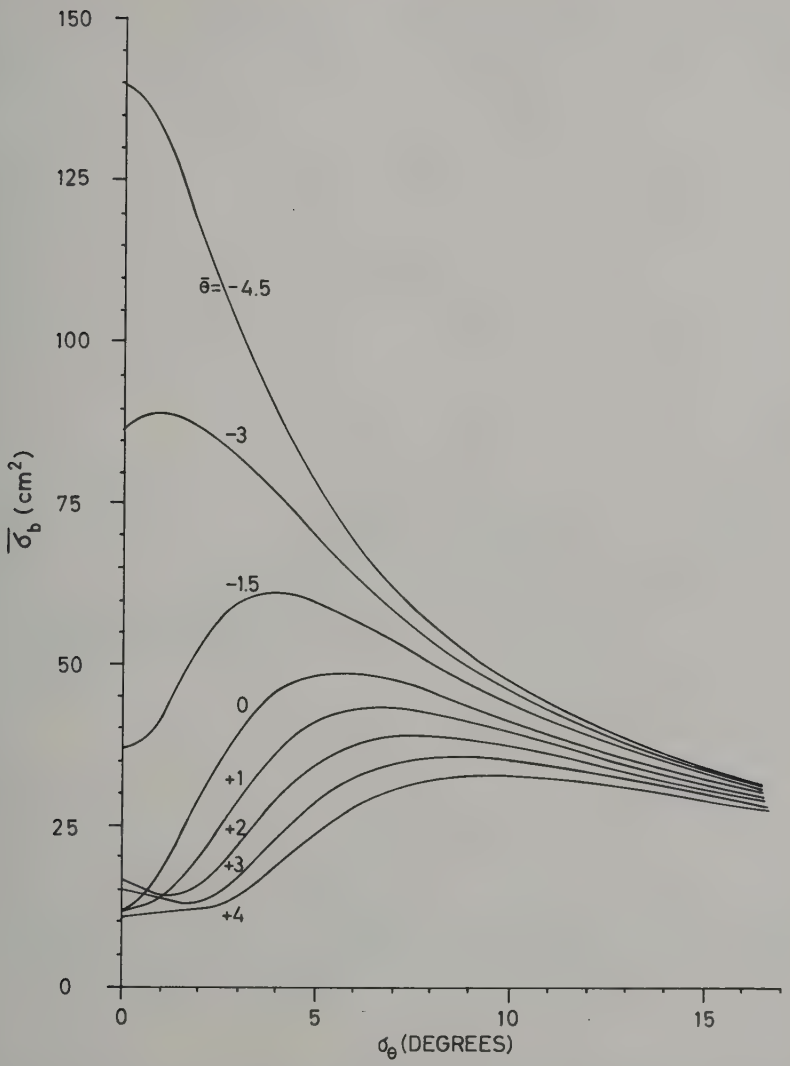

Fig. 5. Mean backscattering cross section $\bar{\sigma}_b$ of saithe in ventral aspect at 38 kHz as a function of the spread σ_θ in tilt angle distribution with mean tilt angle $\bar{\theta}$ as a parameter.

range [–4.5, 4] degrees. The sign convention used consistently throughout this paper is that negative tilt angles denote the head-down position with respect to the true horizontal, while head-up positions are denoted by positive tilt angles.

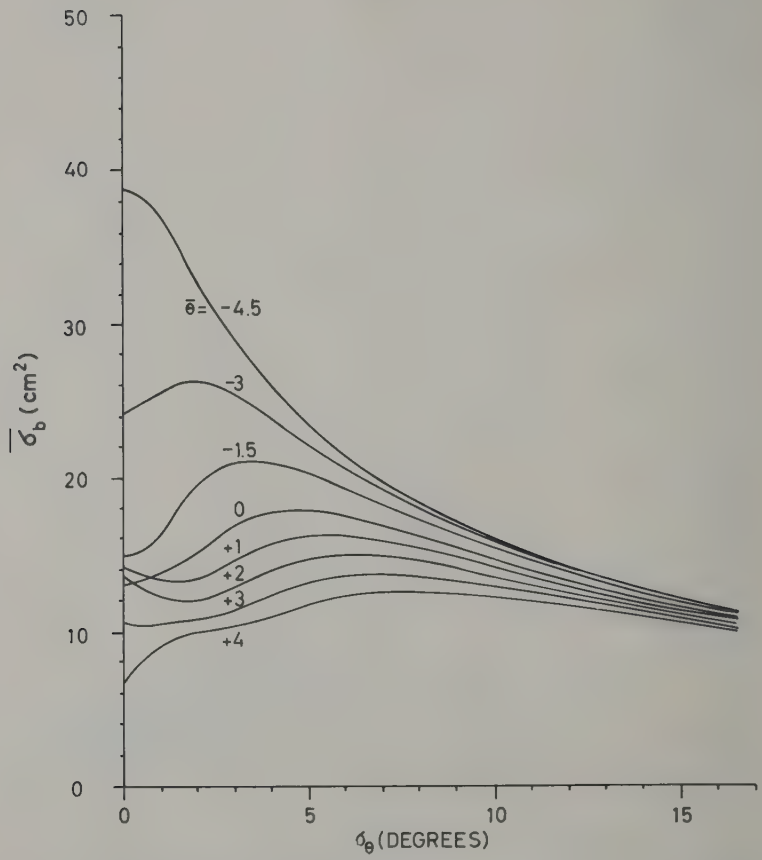

Fig. 6. Mean backscattering cross section $\bar{\sigma}_b$ of saithe in ventral aspect at 120 kHz as a function of the spread σ_θ in tilt angle distribution with mean tilt angle $\bar{\theta}$ as a parameter.

IIIc *Ensemble-averaged extinction cross section*

There is some mention of an extinction cross section for fish in the literature, but mainly in connection with the transmission of sound through fish at or near the frequency of swimbladder resonance (Davies 1973, Ching and Weston 1971, Weston *et al.* 1969). The concept of the extinction cross section is well known in other applications, as in the scattering of light by metallic spheres (Born and Wolf 1970), acoustic scattering by spherical bubbles in water (Wildt 1947), and the scattering of plane scalar fields by

spheres (MORSE and FESHBACH 1953). According to the common definition of these references, the extinction cross section σ_e is the equivalent area normal to the direction of the incident ensonifying signal out of which energy is scattered and absorbed.

For the rather high frequencies used in Røttingen's experiment and for which the two-parameter description of fish scattering behaviour introduced in this study is probably most useful, σ_e may be assumed to be proportional to the surface area of the fish, or of its swimbladder, when projected onto the horizontal plane. If the principal scattering body is represented by an ellipsoid whose length to height to width ratio is designated by the respective dimensions a:b:c, then σ_e as a function of the inclination or tilt angle θ of the body with respect to the horizontal plane is

$$\sigma_e(\theta) = \sigma_{e,o}\sqrt{\cos^2\theta + \varrho^2\sin^2\theta}$$

where $\sigma_{e,o}$ is the value of σ_e at $\theta = 0$ and $\varrho = b/a$ is the ratio of height to length of the scatterer. The effect of roll on σ_e is ignored, which incurs no significant error for cylindriform bodies or quasi-cylindriform bodies which have no extreme roll, which is the plausible assumption for the saithe of Røttingen's experiment.

Given this model for $\sigma_e(\theta)$, the ensemble average $\bar{\sigma}_e$ may now be computed; it is simply the average of $\sigma_e(\theta)$ with respect to the orientation distribution $f(\theta)$, that is,

$$\bar{\sigma}_e = \int \sigma_e(\theta) f(\theta) d\theta$$

where the range of integration is $[\bar{\theta} - \lambda' \sigma_\theta, \bar{\theta} + \lambda' \sigma_\theta]$.

This expression was evaluated numerically for the case $\lambda' = 3$ for saithe having the relative dimensions 17.3:3.2:2.1, which were obtained from RASMUSSEN (1960) and by assuming that the width is two-thirds of the height (NAKKEN pers. com.). It was found that $\bar{\sigma}_e$ could be represented with an accuracy better than 0.1 percent for all $\sigma_\theta \leqq 16.5$ degrees and for all $\bar{\theta}$ in [–5, +5] degrees by the simple quadratic expression

$$\bar{\sigma}_e \doteq \sigma_{e,o}\left[1 - .038\left(\frac{\sigma_\theta}{16.5}\right)^2\right]$$

In the actual evaluation of $\bar{\varepsilon}$ this expression was used, but the variation of $\bar{\sigma}_e$ with σ_θ was found to be entirely negligible, so that $\bar{\sigma}_e$ could have been reduced to the constant $\sigma_{e,o}$, which, however, except in the true ray theory limit, does depend on the center frequency of the ensonifying signal.

IIId. *Connection of spread in orientation distribution and density of fish aggregation.*

It is reasonable to expect σ_θ, or the characteristic measure of spread in the tilt angle distribution of the encaged saithe, to be a monotonically decreasing function of the fish number density ν, for individual fish have less room in which to move, in the mean, as ν increases. It is also reasonable to assume that whatever preference there is for a mean inclination $\bar{\theta}$ should not be affected by the conditions of density, although this is purely speculative. Because of the extreme artificiality of the net cage environment and lack of any preferred direction, as might be established naturally by the fish when schooling (Breder 1959), it is expected that $\bar{\theta}$ would be the neutral inclination, which would be horizontal or nearly horizontal. The entire dependence of the orientation distribution on ν is thus contained in the dependence of σ_θ on ν, which is described below.

Physically σ_θ may be separated into two independent components: that which expresses the biological expectation that σ_θ is a monotonically decreasing function of ν, i.e., that the intrinsic spread in tilt angle decreases with increasing ν, and that which expresses the perspectival effect that the intrinsic, or true, tilt angle generally appears different when viewed from the acoustic source/receiver, which generally is located obliquely, or transversely, with respect to the fish. These two components of σ_θ, which are denoted $\sigma_{\theta,1}$ and $\sigma_{\theta,2}$, respectively, are independent random variables and, as such, are summed in this manner:

$$\sigma_\theta = \sqrt{\sigma_{\theta,1}^2 + \sigma_{\theta,2}^2}$$

As the intrinsic tilt angle distribution of the encaged saithe is unknown, but is expected to be a monotonically decreasing function of ν, the connection between $\sigma_{\theta,1}$ and ν is specified very simply by the model

$$\sigma_{\theta,1} = \sigma_{\theta,1,0} \exp(-\nu/\nu_{cr})$$

where $\sigma_{\theta,1,0}$ denotes the low density limit of the intrinsic spread in tilt angle and ν_{cr}, which is termed the critical density, is the density characteristic of the change in $\sigma_{\theta,1,0}$. Both $\sigma_{\theta,1,0}$ and ν_{cr} are regarded as parameters to be determined or learned by comparison of the results of evaluation of the theoretical $\bar{\varepsilon}$ with Røttingen's observations.

It is expected, however, that $\sigma_{\theta,1,0}$ will be of the order of 16 degrees, which is the figure determined by photographic measurements of cod in the open sea (Olsen 1971), and which could be be thought of as a natural characteristic of cod, and thence of related fish such as saithe. The fact that the saithe are encaged should not lessen confidence in this rough estimate of $\sigma_{\theta,1,0}$ as it applies only in the low density limit where the net cage appears large.

The effect of perspective on altering the intrinsic spread when observed obliquely may be defined through the perspectival spread $\sigma_{\theta,2}$. This is approximately equal to the square root of the average of the mean square tilt angle due to the azimuthal variation in apparent tilt angle relative to an obliquely situated reference point, both with respect to the volume of the net cage, in which the fish are assumed to be randomly homogeneously distributed, and with respect to the transmit and receive beam patterns. In units of degrees

$$\sigma_{\theta,2} = \frac{180}{\pi}\left(\frac{1}{V}\int D_R^2\, D_S^2\, \Delta\chi^2\, dV\right)^{1/2}$$

where $D_R = D_R(\Psi)$ and $D_S = D_S(\Psi)$ are the respective receive and transmit beam patterns in relative units of pressure ratios, which are assumed to be functions only of the polar angle Ψ, and $\Delta\chi^2$ is the variance in apparent tilt angle distribution due to azimuthal variations in orientation. This latter quantity, expressed in units of square radians, is approximated for small mean inclination $\bar{\theta}$ by the expression

$$\Delta\chi^2 = \frac{1}{2\pi}\int_0^{2\pi}\left[\cos^{-1}\left(\sin\Psi\cos\varphi + \frac{\pi}{180}\,\bar{\theta}\,\cos\Psi\right) - \frac{\pi}{2}\right]^2 d\varphi$$

where $\bar{\theta}$ is expressed in degrees. This expression applies properly only in the limit of the highest density, where $\sigma_{\theta,1}$ vanishes, but is adopted here for convenience. D_R and D_S are not equated to unity here as they were earlier in justifiable approximations. They are equated to that beam pattern, expressed in units of relative pressure, which was observed by Røttingen for the transmitter at both 38 kHz and 120 kHz; namely, one which suffers an approximately uniform off-axis degradation which is –1 dB at the outer walls of the net cage. To the first and dominant term, then

$$\sigma_{\theta,2}^2 \doteq .75\left(\frac{180}{\pi}\right)^2 \frac{R^2}{(z_1 + z_2)^2} + .81\,\bar{\theta}^2$$

where R is the radius of the cage and z_1 and z_2, the respective distances from acoustic source to nearer and further surfaces of the cage. If the precise values of these parameters that applied during Røttingen's experiment with saithe are substituted,

$$\sigma_{\theta,2} = \sqrt{4.2 + .81\,\bar{\theta}^2}$$

where both $\bar{\theta}$ and $\sigma_{\theta,2}$ are expressed in units of degrees.

IIIe. *Evaluation of* $\bar{\varepsilon}$

The ensemble-averaged scattering cross sections, $\bar{\sigma}_b$ and $\bar{\sigma}_e$, can now be written, with respect to specific models which connect the parameters of the orientation distribution with ν, the fish number density, as explicit functions of ν. With respect to these same models the ν–dependence of the ensemble-averaged time-integrated echo intensity $\bar{\varepsilon}$ can be determined directly. This was done numerically by means of a digital computer. Some characteristic results of this evaluation, in addition to the principal ones which constitute a quantitative explanation of Røttingen's observations for saithe, are presented in the next section.

RESULTS

The principal results of the quantitative analysis of Røttingen's experiments with saithe are shown in Fig. 7 and 8. In Fig. 7 the result of the evaluation of the theoretical mean or ensemble-averaged time-integrated echo intensity $\bar{\varepsilon}$ for saithe at 38 kHz, according to the approximations described above, and after normalization by the peak value, is presented for the following model parameters: a mean inclination or tilt angle $\bar{\theta} = 0$

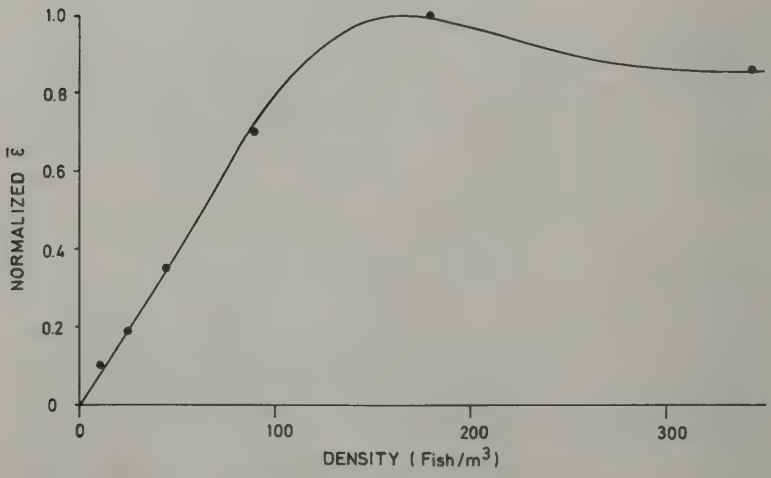

Fig. 7. Comparison of the computed normalized, mean time-integrated echo intensity $\bar{\varepsilon}$ with the mean of Røttingen's observations for saithe at 38 kHz for the following model parameters: $\bar{\theta} = 0$ degrees; $\sigma_{e,o} = 60$ cm^2; $\sigma_{\theta,1,o} = 18$ degrees; $\nu_{cr} = 100$ fish/m^3.

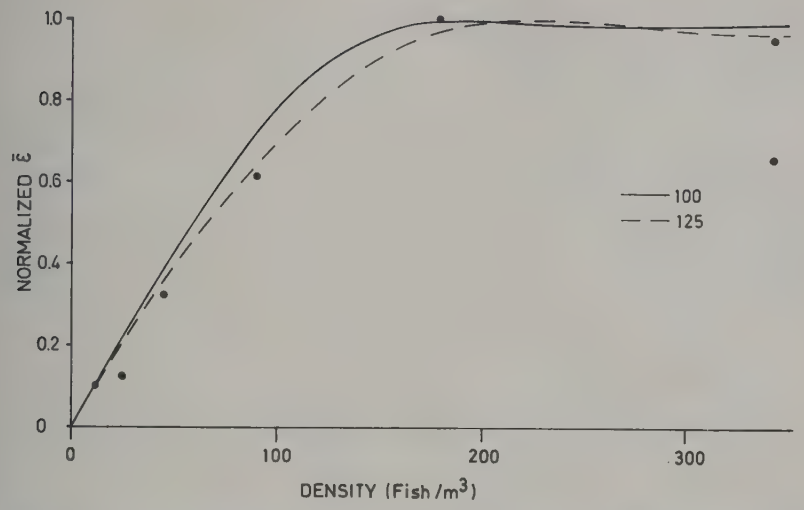

Fig. 8. Comparison of $\bar{\varepsilon}$ with the mean of Røttingen's observations for saithe at 120 kHz for the following model parameters: $\bar{\theta} = 0$ degrees; $\sigma_{e,o} = 100\,\text{cm}^2$; $\sigma_{\theta,1,0} = 18$ degrees; $\nu_{cr} = 100$ and 125 fish/m^3.

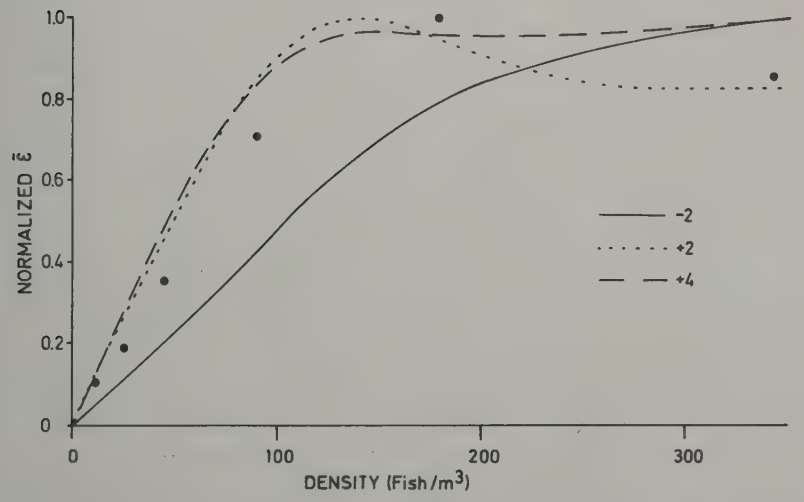

Fig. 9. Dependence of $\bar{\varepsilon}$ on $\bar{\theta}$ for 3 values of $\bar{\theta}$ for saithe at 38 kHz for the following model parameters: $\sigma_{e,o} = 60\,\text{cm}^2$; $\sigma_{\theta,1,0} = 18$ degrees; $\nu_{cr} = 100$ fish/m^3.

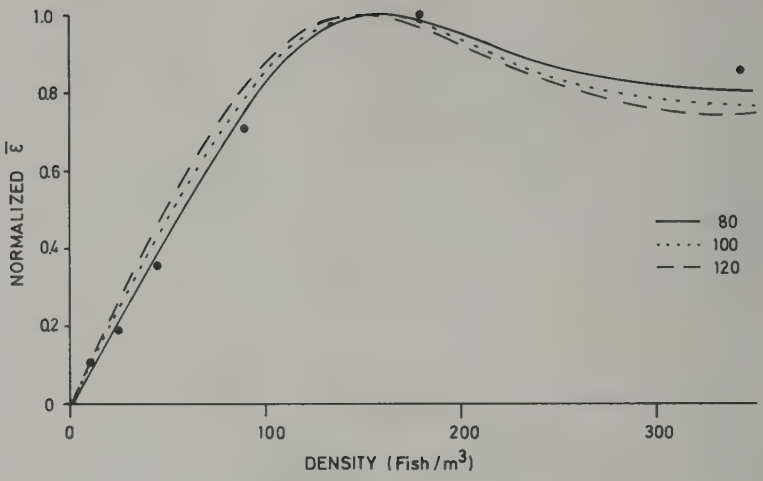

Fig. 10. Dependence of $\bar{\varepsilon}$ on $\sigma_{e,o}$ for 3 values of $\sigma_{e,o}$ for saithe at 38 kHz for the following model parameters: $\bar{\theta}$ = 0 degrees; $\sigma_{\theta,1,0}$ = 18 degrees; ν_{cr} = 100 fish/m^3.

degrees, which describes the horizontal plane; a mean extinction cross section $\sigma_{e,0}$ = 60 cm^2, which is presumed applicable in the limit of high fish number densities; an intrinsic spread in tilt angle distribution at low densities, $\sigma_{\theta,1,0}$ = 18 degrees; and a decreasing exponential ν-dependence of the intrinsic spread in tilt angle distribution which is characterized by the critical density ν_{cr} = 100 fish/m^3. The normalized theoretical $\bar{\varepsilon}$ is computed with respect to these several parameters at a density increment of 10 fish/m^3 over the density range [0,350] fish/m^3, as has been done consistently in Fig. 7 and 12 inclusive, although for different model parameters and thence different peak values and normalizing factors. For purposes of comparison Røttingen's averaged results at 38 kHz, i.e., the average of corresponding values of $\bar{\varepsilon}$ for the two conditions of ensonification at 38 kHz; namely, for pulse durations of 0.3 msec and 0.6 msec; are also presented in Fig. 7, as they are in Fig. 9 to 12 which likewise pertain to computations at 38 kHz.

In Fig. 8 the normalized theoretical estimate of $\bar{\varepsilon}$ at 120 kHz is computed for the same purely geometric model parameters described above for Fig. 7, but for a mean high density extinction cross section $\sigma_{e,o}$ = 100 cm^2. In addition to the computation at ν_{cr} = 100 fish/m^3, a computation at ν_{cr} = 125 fish/m^3 is presented here. The average of Røttingen's observations of $\bar{\varepsilon}$ at 120 kHz, for pulse durations of 0.1 msec and 0.6 msec, are shown at all observed densities except at the highest density. At this density, which is 343 fish/m^3, the respective normalized observations of $\bar{\varepsilon}$ were widely different –

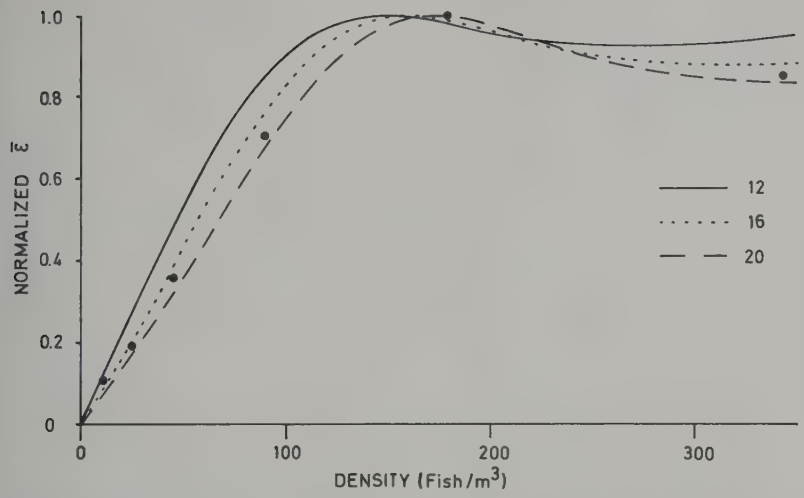

Fig. 11. Dependence of $\bar{\varepsilon}$ on $\sigma_{\theta,1,0}$ for 3 values of $\sigma_{\theta,1,0}$ for saithe at 38 kHz for the following model parameters: $\bar{\theta}$ = 0 degrees; $\sigma_{e,o}$ = 60 cm^2; ν_{cr} = 100 fish/m^3.

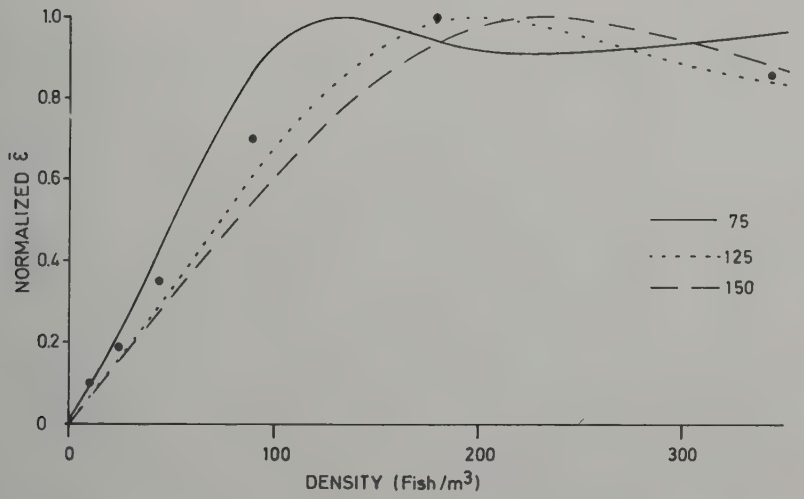

Fig. 12. Dependence of $\bar{\varepsilon}$ on ν_{cr} for 3 values of ν_{cr} for saithe at 38 kHz for the following model parameters: $\bar{\theta}$ = 0 degrees; $\sigma_{e,o}$ = 60 cm^2; $\sigma_{\theta,1,0}$ = 18 degrees.

the only case of its kind as revealed by inspection of Fig. 1 – and are both shown in the figure.

Table 1. Values of parameters of Figures 7 to 12.

Figure number	Center Frequency (kHz)	$\bar{\theta}$ (degrees)	$\sigma_{e,o}$ (cm^2)	$\sigma_{\theta,1,0}$ (degrees)	ν_{cr} (fish /m^3)
7	38	0	60	18	100
8	120	0	100	18	100, 125
9	38	–2, +2, +4	60	18	100
10	38	0	80, 100, 120	18	100
11	38	0	60	12, 16, 20	100
12	38	0	60	18	75, 125, 150

The dependence of the normalized theoretical estimate of $\bar{\varepsilon}$ for saithe at 38 kHz on the several important model parameters; namely, $\bar{\theta}$, $\sigma_{e.o}$, $\sigma_{\theta,1,0}$ and ν_{cr}, are shown in Fig. 9 to 12, respectively. The respective values of each of these parameters in the computation of ε for these figures are presented systematically above in Table 1. Thus in Fig. 9, for example, the dependence of $\bar{\varepsilon}$ on $\bar{\theta}$ is shown for three values of $\bar{\theta}$; namely, –2, +2 and +4 degrees; while the other model parameters adopt the following values: $\sigma_{e,o} = 60$ cm^2, $\sigma_{\theta,1,0} = 18$ degrees and $\nu_{cr} = 100$ fish/m^3. Descriptions of Fig. 7 and 8 are included in the table for ease of reference.

DISCUSSION

The agreement of the theoretical prediction of the normalized mean or ensemble-averaged time-integrated echo intensity $\bar{\varepsilon}$ with Røttingen's averaged observations of $\bar{\varepsilon}$ for saithe at 38 kHz, as shown in Fig. 7, is better than can be expected, or can be justifiably stated without qualification, considering the inherent uncertainty in observations of $\bar{\varepsilon}$ and the uncertainty in representation of the data in a normalized format for such a sparsely sampled density range. Some estimates of $\bar{\varepsilon}$ were stated with confidence intervals in RØTTINGEN (1975), but these were not so significant as to alter the general finding of Røttingen as summarized in Fig. 1 and 2, for saithe and sprat, respectively. That only the averages of the respective observations at 38 kHz for the signals of pulse duration 0.3 msec and 0.6 msec are presented in Fig. 7, and in Fig. 9 to 12, is similarly insignificant, for examination of Fig. 1 shows the separate estimates of $\bar{\varepsilon}$ to correspond very closely. The fact that $\bar{\varepsilon}$ was observed only sparsely for fish number densities in excess of 90 fish/m^3; specifically, only at 179 fish/m^3 and 343 fish/m^3; could be a more serious source of error, but it was a fairly consistent finding of the theoretical work that the $\bar{\varepsilon}$–ν relationship is rather flat over the region of the peak, so the fact that $\bar{\varepsilon}$ was established at only a single density in this region is probably

unimportant. It was also found that the relationship is entirely smooth and often is purely monotonic both above and below the peak, if present, so that a single estimate in the high density region, say about 350 fish/m^3, could be sufficient for determining the gross form of the $\bar{\varepsilon}$–ν relationship. It is assumed, therefore, that despite apparent shortcomings in Røttingen's observations and presentation of $\bar{\varepsilon}$ as a function of ν for saithe, it is a reasonably accurate statement for the true relationship.

If the agreement of theory with experiment at 38 kHz, cf. Fig. 7, is genuine, then evaluation of the postulated model for the same purely geometric, i.e., frequency-independent quantities at 120 kHz, should also produce good agreement with experiment. Observation of the curve with parameter ν_{cr} = 100 fish/m^3 in Fig. 8, for which all geometric quantities have the identical values as in Fig. 7, indicates approximate agreement. Evaluation of the model for the same conditions, but with ν_{cr} = 125 fish/m^3, improves this agreement. As a comparable estimate of $\bar{\varepsilon}$ at 38 kHz for this value of ν_{cr} also yields a fair agreement with experiment, cf. Fig. 12, although not so fine as the estimate obtained with ν_{cr} = 100 fish/m^3, cf. Fig. 7, it may be concluded that the true value of ν_{cr} lines in or near the range 100 to 125 fish/m^3. It is admitted that the single datum at 343 fish/m^3 for a narrowband signal of center frequency 120 kHz and pulse duration 0.6 msec is completely anomalous to a wide range of evaluations of the model, which is why the empirical estimates of $\bar{\varepsilon}$ for saithe at 120 kHz are not averaged for the presentation of Fig. 8 at this particular density, the only density at which such a discrepancy exists throughout the data for saithe, at either frequency. If the two data at 120 kHz at a density of 343 fish/m^3 are both correct, then there is, evidently, a discrimination by pulse duration. This lies beyond the scope of the model, whose development at the outset assumed a certain insentitivity to the pulse duration of the ensonifying signal. That the $\bar{\varepsilon}$–ν relationship may be significantly characterized by the pulse duration of the signal, at least for some center frequencies, is a possibility, and one that might profitably be studied with respect to the larger purposes of the use of acoustic techniques in fisheries research; the present theory simply cannot explain this supposed dependence, which, it is noted, is absent for the sprat of Røttingen's experiment.

The consequence of the consistency in predictions of theory at both 38 kHz and 120 kHz with the corresponding averaged sets of empirical observations, as shown in Fig. 7 and 8, is that the general theory for the process of echo formation by an encaged aggregation of fish, with its two-parameter representation of individual scattering behaviour, is correct. In particular, it may be concluded that the purely geometric models for the orientation distribution of the encaged saithe and for the density dependences of the characterizing parameters of this distribution, on which the $\bar{\varepsilon}$–ν relationship depends crucially, are correct. Thus, the orientation distribution of the

saithe is described satisfactorily by an Olsen-type distribution (OLSEN 1971), i.e., a trucated Gaussian distribution in inclination or tilt angle θ which extends over the range $[\bar{\theta}-\lambda'\sigma_\theta, \bar{\theta}-\lambda'\sigma_\theta]$, where λ' is a constant factor of the order of three and $\bar{\theta}$ and σ_θ are, respectively, the mean and spread of the distribution. For the particular conditions of Røttingen's experiment with saithe, $\bar{\theta}$ is approximately 0 degrees, a constant independent of the fish number density ν, and

$$\sigma_\theta \doteq [\sigma^2_{\theta,1,0}\ exp(-2\nu/\nu_{cr}) + 4.2]^{1/2}$$

where $\sigma_{\theta,1,0}$ is approximately 18 degrees and ν_{cr} is approximately 100 to 125 fish/m^3. The origin of the two factors in this expression has been described fully above.

It was also determined that the maximum ensemble-averaged extinction cross section $\sigma_{e,o}$ for saithe in the ventral aspect is of the order of 60 cm^2 at 38 kHz and 100 cm^2 at 120 kHz. Evidently the pure ray theory limit of acoustics is not entirely applicable to the present problem, so that frequency-dependent variations in the scattering properties of individual fish are to be expected. This is corroborated by comparison of corresponding magnitudes of the ensemble-averaged backscattering cross section at the two frequencies, cf. Fig. 5 and 6.

The ν-dependence of the ensemble-averaged extinction cross section $\bar{\sigma}_e$, through its conjectured dependence on the spread in inclination distribution, is very slight, with only a 3.8 per cent increase in magnitude as σ_θ changes from 16.5 degrees to 0 degrees; that is, presumably, as the density of encaged saithe increases from the approximately free-space value to the highest value. If the computations of $\bar{\varepsilon}$ presented in Fig. 7 to 12 were repeated for density-independent $\bar{\sigma}_e$; specifically for $\bar{\sigma}_e = \sigma_{e,o}$, then the results would be indistinguishable from the corresponding computations with density-dependent $\bar{\sigma}_e$. In view of the influence of the magnitude of $\bar{\sigma}_e$ in determining the form of the $\bar{\varepsilon}$–ν relationship – it predicts merely a monotonic and asymptotic increase to a constant for constant $\bar{\sigma}_b$, cf. Fig. 3, and determines the rate of increase of normalized $\bar{\varepsilon}$ with ν for ν less than about 100 fish/m^3, cf. Fig. 10 – it may be concluded that the ν–dependence of $\bar{\sigma}_e$ is insignificant in determining the general form of the $\bar{\varepsilon}$–ν relationship.

Thus, because the ν-dependence of $\bar{\varepsilon}$ is completely contained in the expression shown above, in section III, which predicts only a monotonic, eventually asymptotic increase in $\bar{\varepsilon}$ with ν for constant $\bar{\sigma}_b$ and $\bar{\sigma}_e$, cf. Fig. 3, and because the ν-dependence of $\bar{\sigma}_e$ is insignificant, the ν -dependence of $\bar{\sigma}_b$ must be of crucial importance in determining the form of the $\bar{\varepsilon}$–ν relationship. This is confirmed by examination of Fig. 9, 11 and 12, which show, respectively, the sensitivities of $\bar{\varepsilon}$ to $\bar{\theta}$, $\sigma_{\theta,1,0}$ and ν_{cr}; that is, to the several purely geometric parameters of the ν -dependent orientation distribution. Variations in any one of these parameters can have a significant effect on the

form of $\bar{\varepsilon}$ through $\bar{\sigma}_b$, whose dependence on $\bar{\theta}$ and σ_θ, thence $\sigma_{\theta,1,0}$ and ν_{cr}, is shown in Fig. 5 for the case of a 38 kHz signal and in Fig. 6 for the case of a 120 kHz signal.

It is noted that $\bar{\varepsilon}$, for constant $\bar{\sigma}_b$ and $\bar{\sigma}_e$, as in Fig. 3, increases linearly with ν for very small ν and begins its asymptotic approach to a constant at comparably low values of ν, which are of the order of 50 fish/m^3 for realistic values of $\bar{\sigma}_e = \sigma_{e,o}$. These latter values are of the order of 60 to 120 cm^2, which are consistent with estimates of σ_b (θ) obtained from empirical target strength data and with knowledge of the physical size of the scatterer. The fact that $\bar{\varepsilon}$ increases linearly to a rather high value of ν, of the order of 100 fish/m^3, is therefore significant. It apparently describes a σ_b which is, at least over this range of ν an increasing function of ν. This dependence of $\bar{\sigma}_b$ on ν is precisely that found at both 38 kHz and 120 kHz by computation from the measured target strength curves of saithe according to the general model in which the orientation distribution is approximately Gaussian in tilt angle and whose variance is a monotnically decreasing function of ν. The similarity in target strength curves at the two frequencies is thus seen to be responsible for the similarity in corresponding $\bar{\sigma}_b$ functions, which is also why the gross forms of the $\bar{\varepsilon}$–ν relationships are similar. If the target strength functions were very dissimilar, then the $\bar{\varepsilon}$–ν relationships also would be expected to be significantly different.

From mere inspection of the data in Fig. 1 and 2 it is difficult to assert that there are frequency-dependent differences in the $\bar{\varepsilon}$–ν relationships. In the neglect of a single datum in Røttingen's observations for saithe at 120 kHz, which was not reproduced in the observations on sprat and which remains unexplained here, what frequency-discrimination there is in the $\bar{\varepsilon}$–ν relationships is attributed to frequency-dependent differences in $\bar{\sigma}_b$ and in the conditions of ensonification of the net cage. For saithe these were found to be slight, but the uncertainty in estimates of $\bar{\sigma}_b$ at 120 kHz was considerable, so the precise form of $\bar{\sigma}_b$ is somewhat uncertain at this frequency. In the computation of the perspectival contribution to the spread in tilt angle distribution it was assumed that there was a slight, identical degradation in both transmit and receive beam patterns at the two frequencies, although this agreement was confirmed experimentally only for the two transmit beams. Admittedly the application of theory to the circumstances of Røttingen's experiment was not entirely consistent, particularly in the treatment of ensemble averages, in which the beam patterns are generally contributing factors. However, it was judged that the several ad hoc approximations used here were reasonable; at least they facilitated the computations of $\bar{\varepsilon}$ without incurring large errors and, in the case of the inferred ν-dependence of $\bar{\sigma}_b$, demonstrated the insignificant role of the beam patterns in determining the ν-dependence of $\bar{\sigma}_b$, and thence the ν-dependence of $\bar{\varepsilon}$.

In summary it is observed that the precise form of the $\bar{\varepsilon}$-ν relationship for the scattering of sound by encaged aggregations of fish, and, presumably, for the scattering of sound by schools of fish, depends on many quantities, which include the backscattering and extinction cross sections as functions of fish orientation, the spatial and orientation distributions as functions of the number density ν, the geometry of ensonification and echo reception, and the signal waveform. While little is presently known about several of these quantities, particularly the extinction cross section and the orientation distribution, much insight into their influence can be gained by the exercise of theory, by calculation of theoretical $\bar{\varepsilon}$ for different postulated models. Comparison of these predictions with observation, as in the present case with respect to Røttingen's measurements of ε for saithe at two different frequencies, can then permit selection of likely models. In particular, comparison of predicted and measured $\bar{\varepsilon}$–ν relationships for fish in a Røttingen-type experiment can permit determination of the mean extinction cross section, a quantity whose measurement is generally complicated, but whose knowledge is essential to determining the precise effect of shadowing in schools of fish.

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APPENDIX

THEORY OF ACOUSTIC SCATTERING BY A COLLECTION OF IDENTICAL SCATTERERS OF RANDOM ORIENTATION AND DISTRIBUTION

Consider a collection of randomly oriented, but otherwise identical scattering bodies which are randomly homogeneously distributed througout a definite region V of a fluid medium of homogeneous density ϱ_o, constant sound speed c_o and negligible background noise. V is ensonified by a narrowband signal $s(t)$, which is emitted by a generally directional source, or transmitting element. The corresponding echo from V is received by a generally directional receiving element, which is essentially collocated with the transmitting element with which it shares a common principal response axis is in the farfield of the source/receiver. The signal waveform $s(t)$ is sufficiently narrowband so that the pressure field modulated by it can be assumed to be attenuated by the free medium at the constant rate α, which is the attenuation constant of the medium at the center frequency of $s(t)$. The pressure due to the source, which is characterized by its value p_o at unit distance from the source, is sufficiently weak so that nonlinear effects can be strictly ignored.

Let the generally complicated scattering behavior of a single scattering body of V be represented by just two parameters: its backscattering cross section σ_b and its extinction cross section σ_e, which are defined with respect to the precise form of $s(t)$ and which generally are complicated functions of scatterer orientation $\hat{r}'$ relative to scatterer position $\underset{\sim}{r}$. The vector $\underset{\sim}{r} = \underset{\sim}{r}_n$ denoting the position of an arbitrary, or the n^{th}, scatterer, and the unit vector $\hat{r}' = \hat{r}'_n$ denoting the orientation of the same body, are defined with respect to a rectangular coordinate system whose origin is situated at the collocated source and receiver and whose z-axis is coincident with the common principal axis of source and receiver. The dependence of the two scattering cross sections on the position $\underset{\sim}{r}_n$ and orientation $\hat{r}_n$ are abbreviated thus:

$$\sigma_b(\underset{\sim}{r}_n, \hat{r}'_n) = \sigma_{b,n} \text{ and } \sigma_e(\underset{\sim}{r}_n, \hat{r}'_n) = \sigma_{e,n}.$$

The echo from V, in the form of the mean or ensemble-averaged time-integrated echo intensity ε, can now be developed directly and expressed as a function of the scatterer number density ν.

In the neglect of other scatterers the pressure field incident on the n^{th} scatterer is that of the free medium, time-retarded wave, viz.

$$\frac{p_o\, s\left(t-\frac{r_n}{c_o}\right)}{r_n} D_{D,n}\, exp\,(-\alpha r_n)$$

where $r_n = |\underset{\sim}{r}_n|$ is the distance from source to position $\underset{\sim}{r}_n$ of the n^{th} scatterer, and $D_{S,n} = D_S(\hat{r}_n)$ is a factor expressing the effect of source directivity on

diminishing the transmitted pressure field in the generally oblique or non-axial direction $\hat{r}_n$ or the n^{th} scatterer. The effect of the presence of other scatterers on this field is its modification by multiple scattering, which might be treated deterministically by the inclusion of the sundry, calculable effects of absorption and refraction internal to the scatterers and reflection and diffraction external to the scatterers, inter alia, but which is treated here simply by the statistical concept of extinction. According to this mode of description, the composite or mutual influence of the scattering bodies in V on the pressure field within V is allowed to be precisely that of a further attenuation of the incident pressure field by scattering and absorption. Since the spatial distribution of the scatterers in V is randomly homogenous, the rate of this attenuation is the net oblique scattering area per unit area of beam. For the n^{th} scatterer this is the quantity $\nu\bar{\sigma}_e|r_n - r_{n,o}|$ where $\bar{\sigma}_e$ is the mean equivalent scattering area, or extinction cross section, which generally is a function of the location χ_n of the n^{th} scatterer, and $r_{n,o}$ is the distance from source to nearest surface of V in the direction $\hat{r}_n$ of the n^{th} scatterer. Thus $|r_n - r_{n,o}|$ is the depth of penetration into V of the incident pressure field at the n^{th} scatterer, and the effect of multiple scattering or extinction is diminution of the incident energy field by the factor

$$exp\ [-\nu\bar{\sigma}_e(r_n - r_{n,o})]$$

The pressure field incident on the n^{th} scatterer, in the mean, is

$$p_{inc,\,n} = \frac{p_o\, s\left(t - \frac{r_n}{c_o}\right) D_{s,n}}{r_n}\, exp\left[-\alpha r_n - \frac{\nu\bar{\sigma}_e}{2}(r_n - r_{n,o})\right]$$

which is just the free-medium, time-retarded wave as modified by multiple scattering within V.

This expression for $p_{inc,n}$ has a precise meaning only in a statistical sense: as the pressure field to be expected at the n^{th} scatterer, at fixed depth of penetration $(r_n - r_{n,o})$, in the mean with respect to the ensemble of all possible, allowed configurations of scatterers in V. It is now temporarily adopted as the description of the actual field at the n^{th} scatterer for an arbitrary particular configuration of scatterers. Later, this ad hoc use will be seen to be justified when the principal quantity of interest, the mean of the integrated echo intensity with respect to the same ensemble of configurations, is computed.

In the formation of the echo from the n^{th} scatterer the incident pressure field is generally distorted. Because this distortion depends on the precise nature of the scatterer and on the conditions of its ensonification, the wave form of the backscattered pressure field is represented by $s_n(t)$. Its strength

relative to the incident field is $\sigma_{b,n}/4\pi$ in the energy domain. When the additional effects of further time retardation, medium absorption and reception by a directional element at the generally non-axial direction $\hat{r}_n$ are included, the contribution to the echo from the n^{th} scatterer may be expressed by

$$p_{sc,n} = \frac{p_o\, s_n\left(t - \dfrac{2r_n}{c_o}\right) D_{S,n}\, D_{R,n}\, \sigma_{b,n}^{1/2}}{\sqrt{4\pi}\, r_n^2} \exp\left[-2\alpha r_n - \frac{\nu\bar{\sigma}_e}{2}(r_n - r_{n,o})\right]$$

Here $D_{R,n} = D_R(\hat{r}_n)$ is the factor describing the effect of the directionality of the receiver on diminishing the received pressure field from the generally non-axial direction $\hat{r}_n$, and $\sigma_{b,n} = \sigma_b(\hat{r}_n)$ is the equivalent backscattering area of the n^{th} scatterer, which is a function of its orientation $\hat{r}_n'$.

The total backscattered field or echo from V after reception, in the proper weak field limit of linear acoustics, is the linear superposition of the several backscattered fields:

$$p_{sc} = \sum_n p_{sc,n}$$

where the summation extends over all νV scatterers in V. The instantaneous intensity $I = I(t)$ corresponding to p_{sc} is the product of in-phase pressure and velocity; thence, by the assumption that $s(t)$ is relatively narrowband,

$$I = \frac{1}{\varrho_o c_o} p_{sc}^2$$

If the signal is of sufficiently short duration T so that the echo from V is completely isolated in time from those echoes produced by extraneous scatterers in the larger medium, such as boundary surfaces, then the time-integrated echo intensity ε; namely,

$$\varepsilon = \int I dt$$

is precisely the energy contained in the echo field of V at the receiving element after effective «shaping» of the echo field by the generally directional receiving element. After appropriate substitution and integration,

$$\varepsilon = \frac{I_o}{4\pi} \sum_{n,m} \frac{D_{S,n}\, D_{S,m}\, D_{R,n}\, D_{R,m}\, \varrho_{nm}\, \sigma_{b,n}^{1/2}\, \sigma_{b,m}^{1/4}}{r_n^2\, r_m^2}$$

$$\times \exp\left[-2\alpha(r_n + r_m) - \frac{\nu\bar{\sigma}_e}{2}(r_n - r_{n,o} + r_m - r_{m,o})\right]$$

where $I_o = p_o^2/\varrho_o c_o$ is a measure of source intensity, and ϱ_{nm} is the cross correlation function

$$\varrho_{nm}(\tau) = \int_{-\infty}^{\infty} s_n(t)\, s_m(t+\tau)dt$$

when evaluated at $\tau = 2(r_n - r_m)/c_o$, which is the difference in arrival times of the echoes from the n^{th} and m^{th} scatterers. Inasmuch as ϱ_{nm} expresses the degree of coherence in the echoes of the $(n.m)$ pair of scatterers, which always irreducibly yields the positive contribution $\varrho(0)$ when $n = m$, ε may be decomposed into two terms, viz.

$$\varepsilon = \frac{I_o}{4\pi}\varrho(0) \sum_n \frac{D_{S,n}^2\, D_{R,n}^2}{r_n^4}\, \sigma_{b,n}\, exp\,[-4\alpha r_n - \nu\bar{\sigma}_e(r_n - r_{n,o})]$$

$$+ \frac{I_o}{4\pi} \sum_{n\neq m} \frac{D_{S,n}\, D_{S,m}\, D_{R,n}\, D_{R,m}}{r_n^2\, r_m^2}\, \varrho_{nm}\, \sigma_{b,n}^{1/2}\, \sigma_{b,m}^{1/2}$$

$$\times exp\left[-2\alpha\,(r_n + r_m) - \frac{\nu\bar{\sigma}_e}{2}(r_n - r_{n,o} + r_m - r_{m,o})\right]$$

which are, respectively, the incoherent and coherent parts of ε, or those terms which are independent of and dependent on the coherence of the constituent fields of p_{sc}.

Evidently, the value of the time-integrated echo intensity ε, through its origin in p_{sc}, is strongly dependent on the precise configuration of scattering bodies in V. Only for those configurations for which $|r_n - r_m| > cT/2$ for all $n \neq m$ will particular ε be independent of coherent contributions. This condition is very strong and, for the kinds of applications that are to be addressed by this calculation, uninteresting. It is assumed, therefore, that the coherent part of ε generally makes a non-negligible contribution for particular configurations of scatterers.

It has been assumed already that the signal waveform $s(t)$ is relatively narrowband and not of very long duration, although, of course, its duration must be long compared to the inverse of its center frequency in order satisfy the condition of being narrowband. In the limit that $s(t)$ is sufficiently narrowband, the power spectra of $s_n(t)$ and $s(t)$ will be very similar and, as a consequence of the Wiener-Khintchine theorem (HORTON 1969), the cross correlation function $\varrho_{nm}(\tau)$ will closely resemble the autocorrelation function $\varrho(\tau)$. If it is assumed further that $s(t)$ is unexceptional and belongs to the class of waveforms which include, for example, pulsed sinusoids and FM

slides of narrow bandwidth, then $\varrho(\tau)$, and correspondingly $\varrho_{nm}(t)$, will oscillate rapidly with τ and contain nearly equal positive and negative parts, so that

$$\int_{-\infty}^{\infty} \varrho_{nm}(\tau)\, d\tau << \varrho(0)T$$

which can be shown by application of the Wiener-Khintchine theorem to the power spectrum of $s(t)$. If the collection of scatterers are randomly distributed in V, then the argument $\tau = 2(r_n - r_m)/c_o$ of ϱ_{nm} for $n \neq m$ will be a stochastic variable and the contribution of the coherent part of ε to the mean of ε with respect to the ensemble of all possible, allowed configurations of scatterers in V will be negligible. In this random-phase-type approximation, then, the mean or ensemble-averaged time-integrated echo intensity $\bar{\varepsilon}$ will be simply the ensemble-average of the incoherent contribution to ε, viz.

$$\bar{\varepsilon} = \frac{I_o \varrho(0)}{4\pi} \sum_n \frac{D_{S,n}^2 \; D_{R,n}^2}{r_n^4} \sigma_{b,n} \exp\left[-4\alpha r_n - \nu \bar{\sigma}_e (r_n - r_{n,o})\right]$$

where all quantities written with an overhead bar are averaged with respect to the ensemble of all possible, allowed configurations of scatterers in V.

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THEORETICAL ESTIMATION OF THE MEAN ECHO INTENSITY — FISH NUMBER DENSITY RELATION FOR ENCAGED SAITHE IN THE DORSAL ASPECT

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ABSTRACT

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The formulation of an earlier theoretical study on the scattering of sound by encaged aggregations of fish (Foote 1978) is applied to the problem of the scattering of sound by an encaged aggregation of saithe when ensonified dorsally. The relationship of the mean time-integrated echo intensity $\bar{\varepsilon}$ and fish number density ν is computed for narrow-band pulsed sinusoidal signals of center frequency 38 kHz and 120 kHz for the same constant geometric and corresponding physical quantities as in the earlier study, but with use of the pertinent dorsal aspect target strength data in place of ventral aspect data. The computed $\bar{\varepsilon}$-ν relationships are compared with the corresponding ventral aspect results as obtained experimentally by Røttingen (1976) and modelled theoretically in Foote (1978).

INTRODUCTION

In a recent paper (Foote 1978) some experimental results on the scattering of ultrasonic sound by encaged aggregations of fish were analyzed. The subject of the analysis, the empirical results of Røttingen (1976), was expressed in the form of relationships of the normalized, mean time-integrated echo intensity $\bar{\varepsilon}$ to fish number density ν. These relationships had been obtained for a range of conditions of ensonification by a pulsed sinusoidal signal for two different kinds of fish, *Pollachius virens* (L.) or saithe, and *Sprattus sprattus* (L.) or sprat. The insensitivity in the forms of the empirical $\bar{\varepsilon}$-ν relationship to both the pulse duration and center frequency of the ensonifying signal for each species of fish was explained qualitatively by purely geometric considerations. A theory was then constructed and applied to the case of the saithe, for which more pertinent scattering data were available than for the case of the sprat.

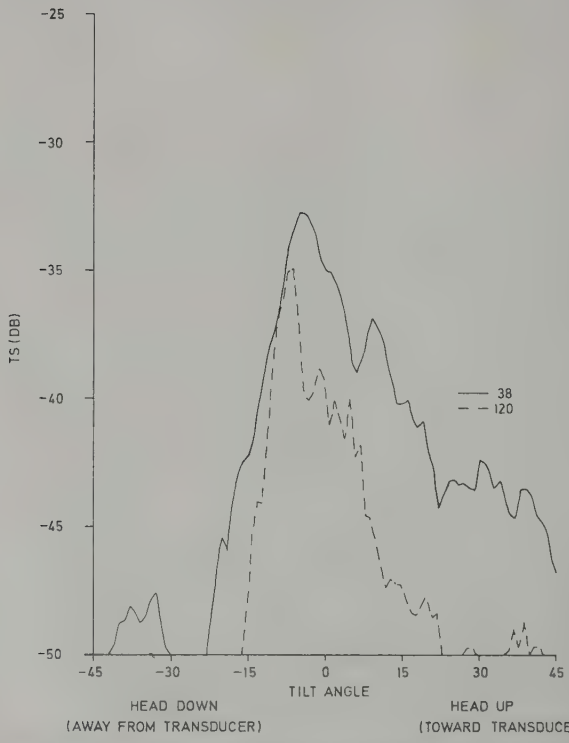

Fig. 1. Dorsal aspect target strength of saithe of mean length 35.1 $\pm$ 0.6 cm at 38 kHz when averaged with respect to 16 specimens, and at 120 kHz when averaged with respect to 17 specimens.

The fish in Røttingen's experiments were ensonfied ventrally in each case, as the transducers were located in a fixed position below the net cage. The corresponding ventral aspect target strength data were used in the quantitative analysis. Because of interest in at-sea applications of this work in fisheries research, where fish are generally ensonified dorsally, an evaluation of the theoretical $\bar{\varepsilon}$-ν relationship for saithe in the dorsal aspect is presented here for the same conditions of ensonification that obtained during the experiments.

METHOD

The evaluation of the theoretical expression for acoustic scattering by an aggregation of fish, as developed and applied in Foote (1978) to the particular circumstances of Røttingen's experiment, proceeds similarly to

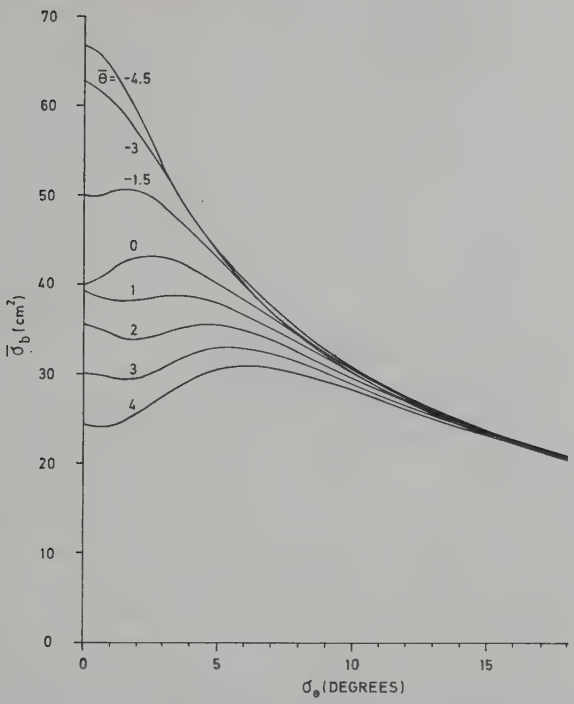

Fig. 2. Mean backscattering cross section $\bar{\sigma}_b$ of saithe in dorsal aspect at 38 kHz as a function of the spread σ_θ in tilt angle distribution with mean tilt angle $\bar{\theta}$ as a parameter.

that of the quoted study. The only difference is that the pertinent dorsal aspect target strength data are used in place of the ventral aspect target strength data.

The new dorsal aspect target strength data for saithe of mean length 35.1 $\pm$ 0.6 cm are shown in Fig. 1. The corresponding ensemble-averaged backscattering cross sections are presented in Fig. 2 and 3 for the respective cases of 38 kHz and 120 kHz. These latter quantities were computed with respect to the identical parameters of the orientation distribution of the earlier study.

RESULTS

The results of the evaluation of the model are shown in Fig. 4 and 5 for the respective cases of 38 kHz and 120 kHz signals. In both figures the same geometric conditions that obtained in Foote (1977) apply. In particular, it was assumed that the mean tilt angle θ of the orientation

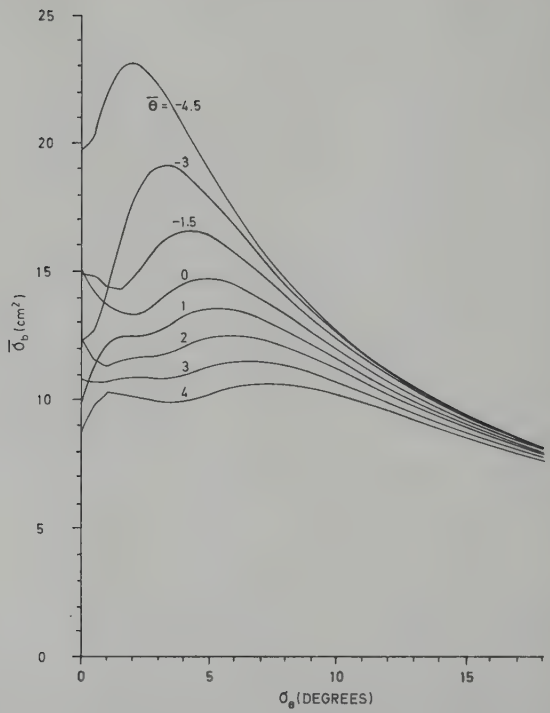

Fig. 3. Mean backscattering cross section $\bar{\sigma}_b$ of saithe in dorsal aspect at 120 kHz as a function of the spread σ_θ in tilt angle distribution with mean tilt angle $\bar{\theta}$ as a parameter.

distribution was 0 degrees and that the mean spread σ_θ in tilt angle distribution has the following form:

$$\sigma_\theta = [\sigma^2_{\theta,1,0} \exp(-2v/v_{cr}) + 4.2]^{1/2}$$

where $\sigma_{\theta,1,0}$, which is the free-space spread in tilt angle distribution, is 18 degrees, and v_{cr}, or critical fish number density, is either 100 or 125 fish/m³. The same extinction cross sections that were used earlier were used here; namely, $\sigma_{e,o} = 60$ cm² for the 38 kHz signal and $\sigma_{e,o} = 100$ cm² for the 120 kHz signal.

DISCUSSION

The predicted normalized $\bar{\varepsilon}$-v relationships for saithe in the dorsal aspect, cf. Fig. 4 and 5, are rather different from the corresponding relationships for the ventral aspect as observed by Røttingen (1976) and

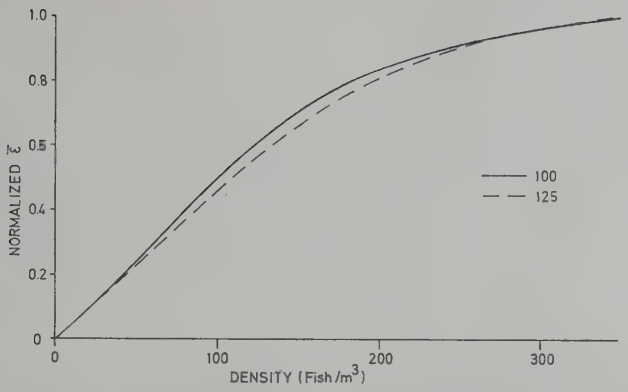

Fig. 4. Theoretical normalized mean time-integrated echo intensity $\bar{\varepsilon}$ as a function of density ν for saithe (in the dorsal aspect) at 38 kHz for the following model parameters: $\bar{\theta} = 0$ degrees; $\sigma_{e,o} = 60$ cm^2; $\sigma_{\theta,1.0} = 18$ degrees; $\nu_{cr} = 100$ and 125 fish/m^3.

reproduced theoretically by Foote (1977). The source of these differences in the case that the corresponding ventral and dorsal aspect extinction cross sections are identical and all geometric quantities remain unchanged, according to theory, lies entirely in differences in the tilt angle dependences of corresponding ventral and dorsal aspect target strength data, thence to differences in the ν-dependences of the corresponding ensemble-averaged backscattering cross sections. These differences are illustrated in Fig. 6 and 7, which show the dependence of $\bar{\sigma}_b$ on the spread σ_θ in tilt angle distribution for a mean inclination of 0 degrees

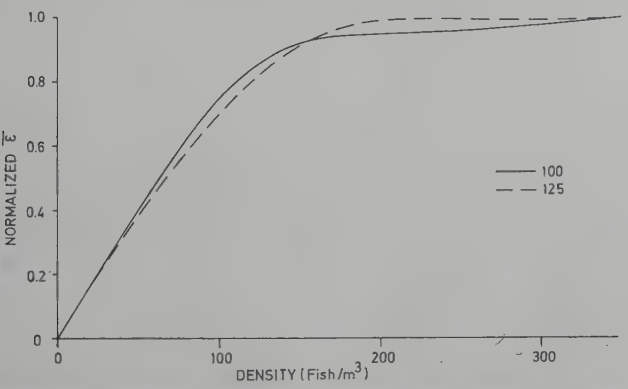

Fig. 5. Theoretical normalized mean time-integrated echo intensity $\bar{\varepsilon}$ as a function of density ν for saithe (in the dorsal aspect) at 120 kHz for the following model parameters: $\bar{\theta} = 0$ degrees; $\sigma_{e,o} = 100$ cm^2; $\sigma_{\theta,1.0} = 18$ degrees; $\nu_{cr} = 100$ and 125 fish/m^3.

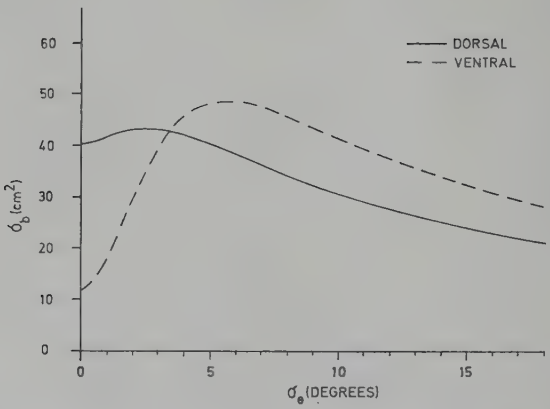

Fig. 6. Mean backscattering cross sections of saithe in dorsal and ventral aspects at 38 kHz as a function of the spread σ_θ in tilt angle distribution for mean tilt angle of 0 degreses.

for signals with respective center frequencies of 38 kHz and 120 kHz. The dorsal aspect curves shown here were extracted from Fig. 2 and 3, while the ventral aspect curves were taken from Fig. 5 and 6 of Foote (1978).

In the case of the 38 kHz signal the difference in behaviour of $\bar{\sigma}_b$ for σ_θ less than 5.5 degrees, cf. Fig. 6, is significant. For these values of σ_θ, which correspond to values of ν greater than about 125 fish/m^3, $\bar{\sigma}_b$ decreases with decreasing σ_θ or, equivalently, with increasing ν for the ventral aspect, while remaining nearly constant for the dorsal aspect. The corresponding $\bar{\varepsilon}$-ν relationships show a definite peaking for ν approximately equal to 160 fish/m^3 in the ventral aspect, and a steady monotonic increase to the maximum computed density, 350 fish/m^3, in the dorsal aspect.

The dependences of $\bar{\sigma}_b$ on σ_θ for the case of a 120 kHz signal are very similar at all values of σ_θ in excess of about 2 degrees. Because the irreducible perspectival contribution to σ_θ exceeds 2 degrees for the particular conditions of Røttingen's experiment, the dependences of $\bar{\sigma}_b$ on ν over the entire range of values of ν can be considered similar for both aspects. Thus the $\bar{\varepsilon}$-ν relationships, after appropriate normalization, are seen to be nearly identical at 120 kHz.

An assumption which has been applied consistently in the computations of this paper is that the dorsal and ventral aspect extinction cross sections are identical. Thus the dorsal aspect extinction cross section has been equated to 60 cm^2 and 100 cm^2 for the respective cases of 38 kHz and 120 kHz signals. It is noted that there is no a priori reason why the dorsal

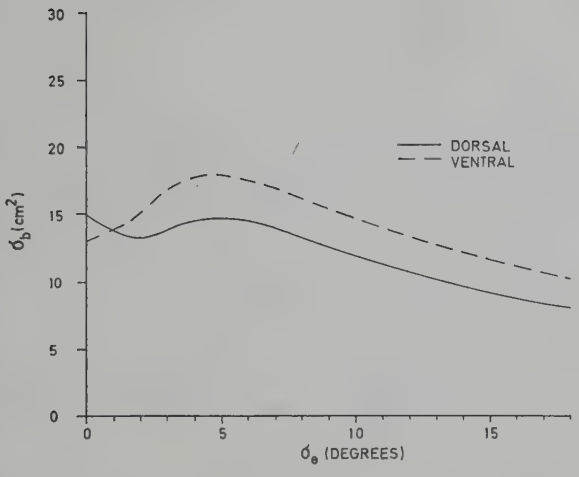

Fig. 7. Means backscattering cross sections of saithe in dorsal and ventral aspects at 120 kHz as a function of the spread σ_θ in tilt angle distribution for mean tilt angle of 0 degreses.

and ventral aspect cross sections should be equal, except in the limit of sufficiently high frequencies. In this limit the pheomenon of scattering is said to become geometric, and the total scattering cross section, thence extinction cross section in the case that absorption within the fish is negligible, is equal to twice the net projected area of the fish. Thus the total scattering cross sections of the fish in ventral and dorsal aspects, and, presumably, the ventral and dorsal aspect extinction cross sections, would be equal.

With respect to the specimens of saithe and signal frequencies of Røttingen's experiment it was found that the characteristic scattering size-to-wavelength ratio was generally much greater than unity, i.e., that the ensonifying frequencies were high. However, the high frequency asymptotic limit evidently did not obtain, for the extinction cross section was observed to depend on frequency. In this case, in which scattering is nongeometric, or frequency dependent, the dorsal and ventral aspect extinction cross sections, like their backscattering cross sections, may be different. The effect of a change in the extinction cross section on the normalized $\bar{\varepsilon}$-ν relationships of Fig. 4 and 5 will be similar to that shown in Fig. 10 of Foote (1977) by virtue of the mathematical equivalence of the quantitative descrtptions of ventral and dorsal aspect scattering.

ACKNOWLEDGEMENT

I. Røttingen, Institute of Marine Research, Bergen, is thanked for providing previously unpublished dorsal aspect target strength data for saithe, and O. Olsen, Department of Physics, University of Bergen, for his help in analyzing them. The financial support of the Royal Norwegian Council for Scientific and Industrial Research is acknowledged.

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VARIATIONS IN ZOOPLANKTON VOLUMES AT THE PERMANENT OCEANOGRAPHIC STATIONS ALONG THE NORWEGIAN COAST AND AT WEATHERSHIP STATION M(IKE) IN THE NORWEGIAN SEA DURING THE YEARS 1949—1972

By

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ABSTRACT

Wiborg, K.F. 1978. Variations in zooplankton volumes at the permanent oceanographic stations along the Norwegian coast and at weathership station M(ike) in the Norwegian Sea during the years 1949—1972. *FiskDir. Skr. Ser. HavUnders.*, *16*:465—487.

During the years 1949—1972 zooplankton was sampled in vertical hauls at permanent oceanographic stations along the coast of Norway and at the weathership station «M» in the Norwegian Sea. During 1949—1962 (station M:—1965) Nansen net «8/72» was used, later the Juday net, J.36. The Juday net was found to catch more plankton in relation to the opening of the net.

During May—August average plankton volumes were larger off northwestern Norway than farther south.

Deviations from the long term averages in plankton volumes were compared with observations from adjacent areas of the North Sea, Norwegian Sea and Barents Sea. Some similarities were found, but local variations seem to be the major cause of observed differences.

No clear relationship was established between zooplankton biomass and sea temperature.

Rich year classes of cod seem to be born more frequently in years when zooplankton biomass is above average, while medium and poor year classes are possibly more frequent in years with lower abundance of plankton, but the data are not sufficient for a conclusion.

No correlation was found between abundance of plankton and of cod larvae.

INTRODUCTION

Since 1949 the composition and quantities of zooplankton along the coast of Norway and in the Norwegian Sea have been described in a number of reports (LIE 1961, 1966, 1968, WIBORG 1954, 1955, 1958, 1960 a and b, 1976). This paper deals with variations in zooplankton volumes at the permanent oceanographic stations and at station M during the years 1949—1972.

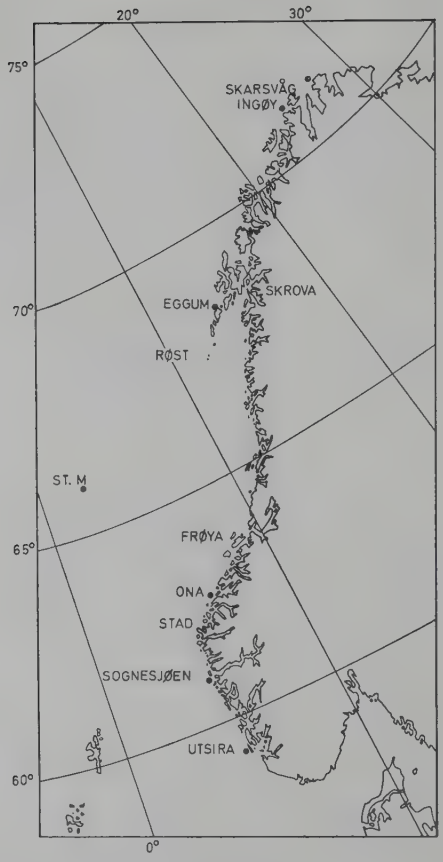

Fig. 1. Permanent zooplankton stations 1949—1972.

MATERIALS AND METHODS

Zooplankton has been sampled in vertical hauls from the bottom to 0 m and from 50 to 0 m at permanent oceanographic stations along the coast of Norway (Fig. 1) at intervals from one week to one month since 1949. At weathership station M in the Norwegian Sea (lat. 66°00′ N, long. 02°00′ E) samples have been taken weekly from 100 to 0 m and during some years also from 25 to 0 m. Here, a 600—100 m haul was also taken once a month and since September 1959, once a week.

During 1949—1965 a Nansen net (opening diameter 70 cm, mesh size

approx. 180 μ, Dufour bolting silk No. 8) was used, to be replaced by the Juday net, (diameter 36 cm, mesh size 180 μ, Nytex nylon gauze). The net was not changed simultaneously at all stations and was shifted last at station M.

Plankton volumes were measured after removal of large organisms such as salps and medusae, until 1970 by draining (WIBORG 1954) and later by displacement (ROBERTSON 1970). A comparison indicated slightly higher figures for draining, and a correction factor of 0.75 was calculated and used for the earlier figures from draining.

According to BOGOROV (1959) the Juday net catches up to twice as many organisms per 1 m^3 as the Nansen net. In the present investigation the displacement volumes in relation to the net opening were also larger in the Juday net hauls. TRANTER and SMITH (1968) assumed that the tropical Juday net, which is a scaled up version of the ordinary Juday net, might have an initial efficiency of more than 100% because of its non-porous reduction cone, and that the probability of clogging could be high in tows longer than 50 m in water rich in plankton. In order to test the effect of the reduction cone a Juday net similar to those used in the present investigation was equipped with a Tsurumi-Seiki flowmeter placed halfway between the sentre and the rim (ANON. 1968 p. 156) and suspended from a bar, one end of which extended well outside the rim of the net. Another flowmeter was fastened at this end. The unit was twice towed round a circular tank for a distance of approximately 180 m at a speed of 1.0 m/sec. and 0.8 m/sec. The reading of the flowmeter indicated a filtration of 83.2% of the water offered. Vertical hauls were taken in September 1977 in the sea near Bergen at a speed of 0.5 m/sec. In five 20-0 m hauls the percentages of filtration were, 73.8, 88.3, 88.3, 88.3, and 90.2; average 85.8%. In four 200-0 hauls, 62.8, 67.0, 68.7, 71.0, average 67.4%. In two 300-0 hauls, 65.1, 67.7, average 66.4%. Thus it is evident that the initial filtration of the Juday net is below 100% and that the percentage of filtration may decrease further with increasing length of the haul if plankton is abundant. No flowmeter tests are available for the Nansen net.

In the present investigation no correction factor has been used for filtration. Accordingly, volumes of plankton per unit of sea surface are minimum figures.

RESULTS

AVERAGE MONTHLY ZOOPLANKTON VOLUMES DURING 1949—1972

The monthly average plankton volumes during 1949—1972 are shown in Fig. 2 and Table I, p. 484. The Juday net figures are generally higher, and are considered to give a more reliable picture of the plankton quantities.

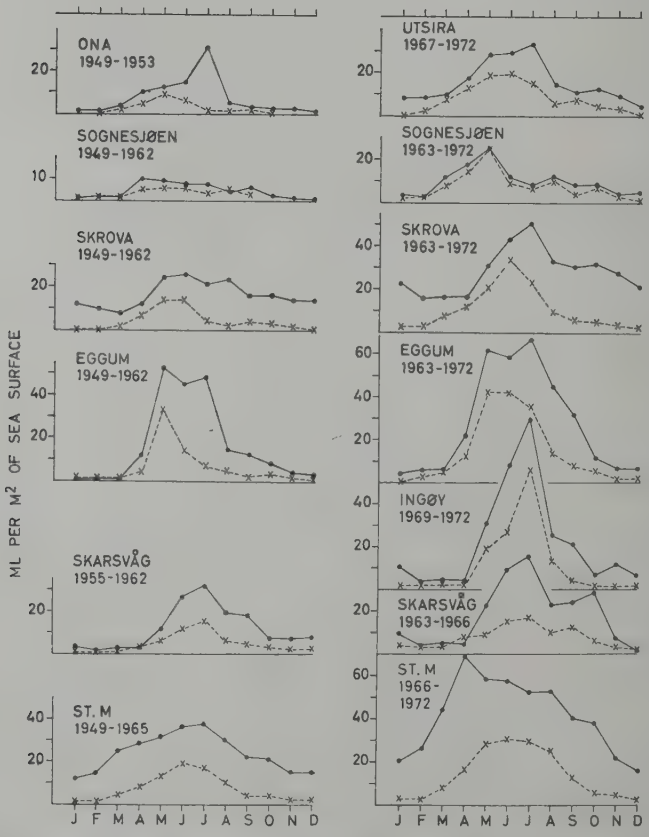

Fig. 2. Average annual variations in displacement volumes of zooplankton at permanent stations along the coast of Norway and at station M 1949—1972. Left) Nansen net hauls, right) Juday net hauls. Monthly mean figures per m² of sea surface. Dashed) 50-0 m, solid) bottom to 0 m (station M 100-0 m and 600-0 m).

Utsira

Sampling started in 1965 though samples were not regular until 1967. The spring increase starts at the end of March with maximum volumes occurring in June—July. These were of about 30 ml/m² in the total hauls and 20 ml/m² in the upper 50 m. Small increases have been observed in September—October.

Sognesjøen

Plankton volumes were small when compared to those of the other stations. The bottom is at 300 m, but hauls were only taken from 200 m, and some plankton may not have been sampled due to it staying below this depth, especially from autumn to spring. The spring increase starts in March—April though during 1949—1962 the average volume did not change very much from April to July. There was a second increase in August—September.

During 1963—1972 the peak in May was more pronounced with a maximum of 25 ml/m².

Ona

Complete data are only available from 1949 to 1953. The spring increase started in March—April, the main maximum in the upper 50 m occurring in May and in the total water column, in July.

Skrova

The spring increase started in April—May. During 1949—1962 the plankton of the upper 50 m was most abundant from May to June and in the total hauls from May to August. A second peak was indicated in September—October. During 1963—1972 the total volume had a main peak of 50 ml/m² in July while the 50-0 volume was at a maximum of 34

Table 1. Average biomass of zooplankton from 0 to 50 m in the eastern Norwegian sea (Norwegian Current) in June 1958 (mg/m³). From Gruzov and Pavshtiks (1961), Timokhina (1963, 1972).

Section	1958	1959	1960	1961	1962	1965	1966	1967	1968	1969	1970
71°10′ N	1183	831	1464	1240	1154	960	1480	—	1220	1870	1223
69°20′ »	1736	1100	1160	1230	1528	1180	1684	1820	1480	1444	830
67°30′ »	—	—	1256	735	818	2040	3000	2080	2500	1370	1014
65°45′ »	—	—	—	—	1346	2320	1840	1040	1620	574	1600
63°00′ »	—	1070	920	552	1204	1200	1340	840	846	1407	1134
60°04′ »	—	1406	940	—	636	1240	—	—	1432	1056	822

ml/m² in June. During winter the plankton was relatively abundant, 15—22 ml/m², probably an accumulation effect due to the topography of the Vest fjord.

Eggum

The variations have been characterized by small volumes during late autumn and winter and distinct peaks in May—July. Volumes have been larger than at Skrova, maxima in 1963 were 60—67 ml/m² for the total hauls and 42 ml/m² in the upper 50 m.

Skarsvåg—Ingøy

The spring increase starts in April—May, the main maximum occurring in July and a second peak in September. In 1963—1966 the average maximum volumes were 37—45 ml/m². After three years without plankton sampling at the Skarsvåg station, it was replaced by Ingøy in 1969 with complete sampling from July 1969 to August 1972. The high peak in July (Fig. 2) was caused by one sample of 165 ml/m² in July 1970.

Station M

The spring increase starts in February—March. For the 1949—1965 period the peak for the 100-0 m hauls reached in May, for 600-0 m in July, and during 1966—1972 the maxima for both intervals were reached in April. Plankton was relatively abundant in the upper 100 m until July and in the upper 600 m until October.

AVERAGE ZOOPLANKTON VOLUMES DURING MAY—AUGUST

Averages have been worked out per month for the period May—August when the plankton generally is most abundant (Fig. 3).

The larger figures calculated for the Juday net hauls are immediately apparent, but the ranging in biomass at the stations is more or less the same, viz. Eggum, station M, Skrova, Skarsvåg and Sognesjøen. During the period 1949—1962 Ona ranged before Sognesjøen as did Utsira during 1963—1972.

The 50-0 m volumes were about half the total volume or below, except at Sognesjøen where the deeper layers may have been sampled insufficiently. At station M the 100-0 m volumes where of nearly the same size as the 50-0 m volume at Eggum.

It is assumed that the 1963—1972 figures give a relatively correct picture of the average quantities of plankton during May—August at Eggum and station M, *i.e.* 50—60 ml/m², at Skrova and Skarsvåg 30—40 ml/m², at Sognesjøen and at Utsira 15—25 ml/m².

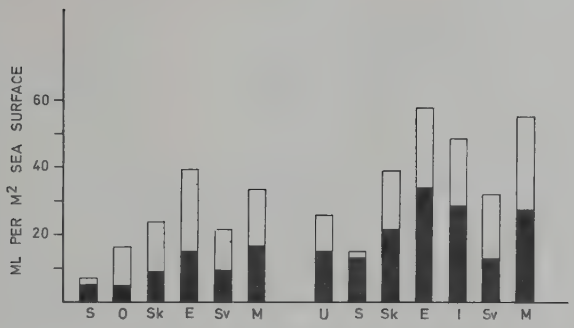

Fig. 3. Average monthly zooplankton volumes during May—August. Left) Sognesjøen (S), Skrova (Sk) and Eggum (E) 1949—1962, Ona (O) 1949—1954 Skarsvåg (Sv) 1955—1962, station M 1949—1965. Right) Utsira (U) 1967—1972, Sognesjøen, Skrova and Eggum 1963—1972, Ingøy (I) 1969—1972, Skarsvåg 1963—1966, station M 1966—1972. Total column) bottom to surface, black column) 50-0 (station M 600-0 m and 100-0 m).

DEVIATIONS FROM THE MEAN MONTHLY AVERAGES DURING THE YEARS 1949—1972

Fig. 4—10 show deviations from the mean plankton volumes for each month and for the period April—August during the years 1949—1972 (Table I). In some years data are incomplete, lacking for one to several months or even years. For this reason the period April—June has been used for station M instead of April—August. The figures have therefore to be considered with reservation.

The deviations in a particular year are seldom similar at two or more stations. During 1950 positive deviations occurred in June at Eggum and station M, and in August at Ona, Skrova, Eggum and station M. In

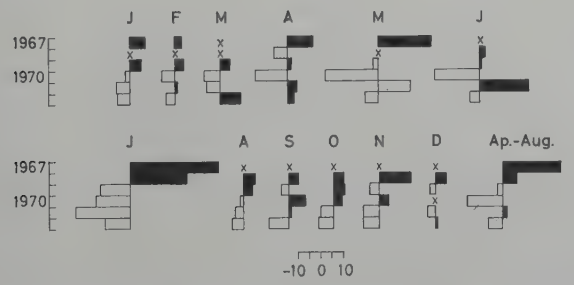

Fig. 4. Utsira. Deviations from the mean zooplankton volumes for each month of the year and of the period April—August 1967—1972. x) No observations.

Fig. 5. Sognesjøen. Deviations from the mean zooplankton volumes for each month of the year and of the period April-August during 1949 - 1972. x) No observations.

1965 there were positive deviations in June, July and August at Skarsvåg and station M. In 1966 deviations were common in June at Sognesjøen, Skrova and Eggum, and in July at Sognesjøen and Skrova.

DISCUSSION

COMPARISON OF ZOOPLANKTON IN ADJACENT AREAS

During April 1962 and April—May 1963 zooplankton was very abundant on the coastal banks off Stad—Frøya on the west coast of Norway (Wiborg 1976), but scarce at the permanent station at Sognesjøen. At Eggum the biomass was below average during April—May 1962, but above average in May 1963. During April—May 1964 zooplankton was abundant over all coastal banks between Stad and Røst (Wiborg 1976) and at Sognesjøen and Eggum.

Longhurst *et al.* (1972) reported on annual fluctuations in abundance of various plankton organisms west of the British Isles and in the North

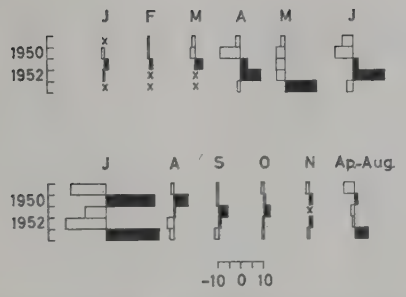

Fig. 6. Ona. Deviations from the mean zooplankton volumes for each month of the year and of the period April—August 1949—1953. x) No observations.

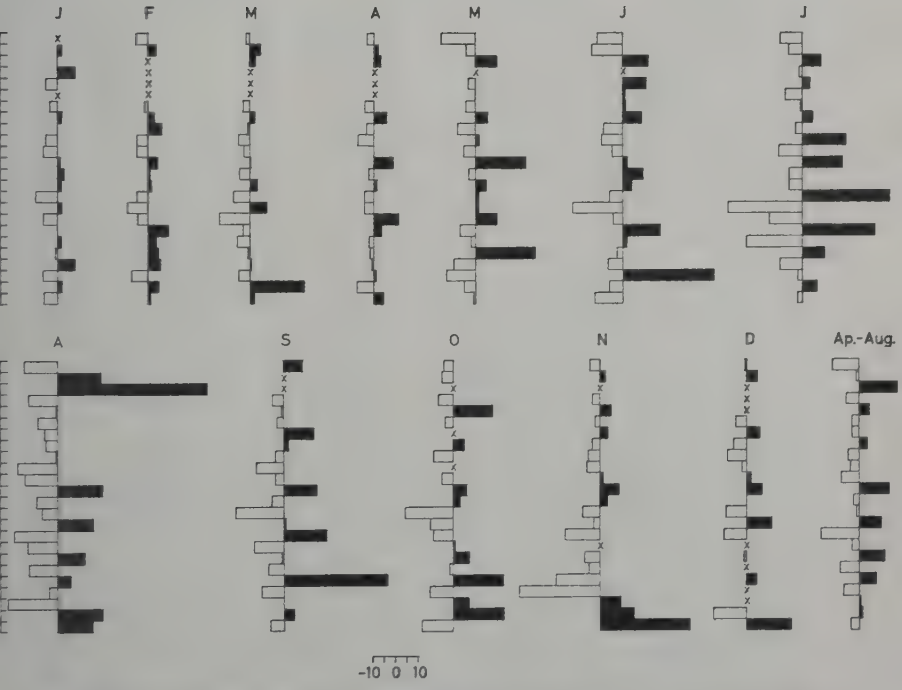

Fig. 7. Skrova. Deviations from the mean zooplankton volumes for each month of the year and of the period April—August 1949—1972. x) No observations.

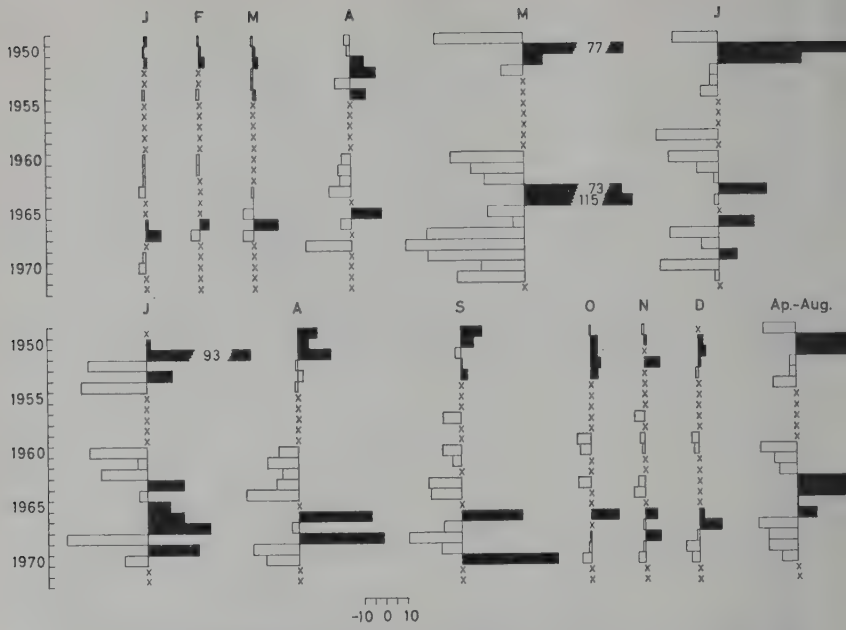

Fig. 8. Eggum. Deviations from the mean zooplankton volumes for each month of the year and of the period April—August 1949—1972. x) No observations.

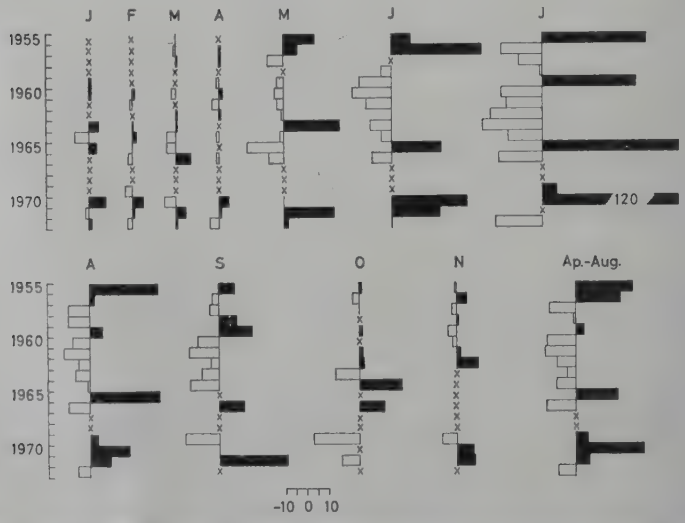

Fig. 9. Skarsvåg and Ingøy. Deviations from the mean zooplankton volumes for each month of the year and of the period April—August 1949—1972. x) No observations.

Fig. 10. Station M. Deviations from the mean zooplankton volumes for each month of the year and of the period April—June 1949—1972. x) No observations.

Sea during the years 1949—1970. In the North Sea the number of *Calanus* sp. fluctuated in very much the same way as in the figures for April—August at Sognesjøen, with peaks in 1952 and 1964 and large reductions in 1958, 1962 and 1965 (Fig. 11).

The biomass and composition of the zooplankton in the Norwegian Sea have been studied for a number of years by Soviet scientists. Most of the samples were collected in June in the eastern part of the area in sections along the parallels between 60°N and 74°N. Biomass was calculated as mg/m³ of zooplankton in 50-0 m. Data from Gruzov and Pavshtiks (1961), and Timokhina (1963, 1972) are compiled in Table 1. The two northern sections may be compared with Skarsvåg and Ingøy, the median ones with Skrova and Eggum and the two southern sections with Sognesjøen. There does not seem to be any common trend in the variations of abundance among the sections, neither do they correspond with any of the coastal stations in their variations.

Timokhina (1968) calculated the average annual biomass of *Calanus*

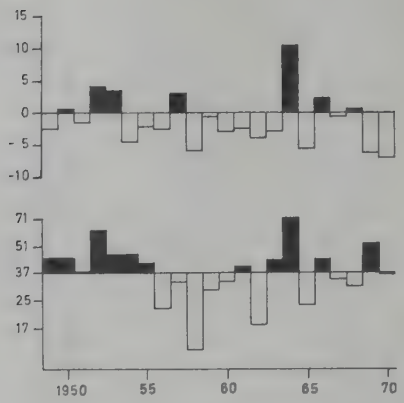

Fig. 11. Deviations from the mean monthly zooplankton volumes for the period April —August at Sognesjøen 1949—1970 compared with variations in relative abundance of *Calanus* sp. in the same years, redrawn from LONGHURST *et al.* (1972).

finmarchicus in coastal waters off western and northern Norway during 1959—1963. The figures were as follows (tons per km²): 1959, 19.5; 1960, 14.4; 1961, 2.8; 1962, 12.4; 1963, 22.0.

A zooplankton biomass above average was recorded at station M and Skrova during April—August 1960 and at station M, Skrova and Eggum during the same period in 1963. At Skarsvåg the biomass was above average in 1959, but below during 1960—1963.

CORLETT (1965) studied zooplankton in the western Barents Sea during the summers of 1949—1959. The biomass was relatively high in 1949, 1950, 1954 and 1957—1959, but low in other years (see Table 4, p. 00). Similarities to the Eggum and Skarsvåg results thus occurred in 1950, 1952, 1953, 1958 and 1959.

During the years 1951—1958 ZELIKMAN and KAMSHILOV (1960) observed a small biomass in the southern Barents Sea in 1952, maxima in 1951 and 1954, and also high figures in 1955—1957. At Eggum and Skarsvåg the April—August figures were similar in 1951, 1952, 1955 and 1956.

ANTIPOVA, DEGTYAREVA and TIMOKHINA (1974) observed peaks in abundance of zooplankton biomass in the southern Barents Sea in May 1950, 1959, 1960, 1961 and 1967, and in July 1950, 1953, 1962 and 1964.

Zooplankton thus seems to have been commonly very abundant both off the northwestern coast of Norway and in the western, or southern, or in both areas of the Barents Sea during the spring and summer months of 1950, 1951, 1955, 1956 and also in July 1953. A biomass below average was common in 1952.

ZOOPLANKTON AND SEA TEMPERATURE

Zelikman and Kamshilov (1960) did not find any clear relationship between the abundance of zooplankton and sea temperature.

Antipova, Degtyareva and Timokhina (1974) observed a positive correlation between the temperature of the sea in April and May and the biomass of zooplankton along the Kola section in the southern Barents Sea. They concluded that the warming of the upper water layers stimulated the growth of phytoplankton which in turn influenced the development of the zooplankton. Furthermore, the heat content of the upper water layers might also stimulate the development of the gonads of *Calanus finmarchicus*. For June, July and September there was no positive correlation, probably because *Calanus* then descended to deeper layers to hibernate.

Midttun (1969, 1975) studied the annual variations in the sea temperature at the permanent oceanographic stations along the Norwegian coast during 1945—1965 and also surface temperatures at other coastal stations during 1936—1970. At Eggum maxima in temperatures were observed in 1950, 1961, and 1964 while surface maxima occurred in 1967 and 1970. Plankton biomass above average was observed in 1950 and 1964, but also in 1963 and 1966 when the temperature was low. Near Skarsvåg there were temperature maxima in 1959—1961 and minor peaks in 1964, 1967 and 1969—1970. Zooplankton biomass was slightly above average in 1959 and 1970 whereas the other peaks coincided with low sea temperatures.

The simultaneous occurrence of high sea temperatures and above average plankton biomass seems therefore to be rather accidental. It should, however, be noted that in 1950 there was a more general abundance of plankton at several localities, both at station M, Eggum, and partly at Ona and Skrova.

ZOOPLANKTON BIOMASS, ABUNDANCE OF COD LARVAE OFF THE NORTHWESTERN COAST OF NORWAY, AND THE SIZE OF THE YEAR CLASSES OF ARCTO-NORWEGIAN COD

Deviations from the mean of the zooplankton biomass at Skrova, Eggum and Skarsvåg during April—August are compared in Table 2 with the relative abundance of cod larvae during May—July 1949 –1972 and with the strength of the same year classes of cod at an age of 2 + years. Data on cod larvae have been taken from Baranenkova (1974), Dragesund and Hognestad (1967), Hognestad (1969 a, b, and c, 1971, 1972, 1973), Smestad and Øyestad (1974) Wiborg (1957, 1960) and on year classes of cod from Ponomarenko (1976) and Anon. (1976).

Table 2. Occurrence of cod larvae off northern Norway, number of cod of 2+years/hour of trawling in the Barents Sea, and abundance of zooplankton at Skrova (S), Eggum (E) and Skarsvåg-Ingøy (Sk) during April—August 1949—1972. +) at or above average, ÷) below average, ×) no observation. R-rich, M-medium, P-poor. See text, p. 477-478

Year	Cod larvae		Cod, 2 + years No./hr of trawling	Zooplankton abundance		
	Apr.—June	June—July		S	E	Sk
1949	+	×	24 M	÷	÷	×
1950	÷	×	75 R	+	+	×
1951	÷	×	6 P	+	+	×
1952	+	×	3 P	÷	÷	×
1953	÷	×	9 P	+	÷	×
1954	+	×	6 M	÷	÷	×
1955	+	×	9 P	÷	×	+
1956	+	×	14 M	+	×	+
1957	÷	×	13 M	÷	×	÷
1958	+	×	19 M	÷	×	+
1959	+	÷	10 M	÷	×	+
1960	÷	÷	13 M	+	÷	÷
1961	÷	+	2 P	÷	÷	÷
1962	+	+	6 M	+	÷	÷
1963	÷	+	76 R	+	+	÷
1964	÷	÷	46 R	÷	+	÷
1965	÷	÷	1 P	÷	÷	+
1966	÷	÷	1 P	+	+	÷
1967	÷	÷	1 P	÷	÷	×
1968	÷	÷	5 P	+	÷	×
1969	÷	÷	9 P	÷	÷	+
1970	+	+	79 R	+	÷	+
1971	+	×	32 R	+	÷	+
1972	+	×	35 R	÷	×	+

The abundance of cod larvae has been classified very roughly as high (+) or low (—). Year classes of cod with 30—79 specimens per hour of trawling are characterized as rich, those with 10—29 per hour as medium and those below 10 per hour as poor. The year classes of 1954 and 1962 have been adjusted to medium according to Anon. (1976).

The figures do not lend themselves to detailed statistical analysis, but in order to get a rough idea of the relationships, the data have been arranged as shown in Tables 3—6.

Rich year classes of cod seem to be born more frequently in years when zooplankton biomass is above average while medium and poor year classes are possibly more frequent in years with low abundance of plankton, but as data are lacking for a number of years, the conclusion is uncertain.

Table 3. Number of instances where zooplankton biomass was at or above average (+) or below average (÷) at Skrova, Eggum and Skarsvåg-Ingøy during April-August and year classes of cod aged 2 + years in the Barents Sea for the years 1949—1972. ×) no observation. Data from Table 2.

Cod Year-class	Zooplankton											
	Skrova		Eggum			Skarsvåg-Ingøy			Total			
	+	÷	+	÷	×	+	÷	×	+	÷	×	
Rich	4	2	3	2	1	3	2	1	10	6	2	
Medium	3	6	0	5	4	4	3	2	7	14	6	
Poor	4	5	2	6	1	2	2	5	8	13	6	

Corlett (1965) found a high positive correlation between the summer biomass of zooplankton in the western Barents Sea and the relative strength of the corresponding year classes of cod. His data have been used in Table 4 together with the figures from Eggum and Skarsvåg for the same period. Only 6 of the 11 observations of zooplankton above or below average correspond with the figures of relative strength of the cod year classes. This may indicate that the size of the year classes is partly determined after the cod fry have left the coastal areas of northern Norway.

Sysoeva (1973) studied the feeding and survival of the Barents Sea cod larvae. She concluded that the number of cod larvae in June—July did not depend on the number of eggs and larvae in April—May, but was determined by the survival from April—May to June—July. This sur-

Table 4. Year-classes of cod and zooplankton biomass in the western Barents Sea during summer (CORLETT 1965), and at Eggum-Skarsvåg in 1949—1959. Data and symbols as in Table 2.

Year	Year-class cod	Zooplankton mg/m³	Zooplankton Eggum-Skarsvåg
1949	M	47	÷
1950	R	54	+
1951	P	15	+
1952	P	22	÷
1953	P	26	÷
1954	M	46	÷
1955	P	24	+
1956	M	29	+
1957	M	34	÷
1958	M	45	+
1959	M	35	+

Table 5. Number of cases where abundance of zooplankton was above (+) or below (÷) average, and abundance of cod larvae above (+) og below (÷) average in April–June and June–July at Skrova, Eggum and Skarsvåg. ×) no observation. Data from Table 2.

Cod larvae	Skrova		Eggum			Skarsvåg			Total		
April–June	+	÷	+	÷	×	+	÷	×	+	÷	×
+	4	7	0	6	5	7	1	3	11	14	8
÷	7	6	5	7	1	2	6	5	14	19	6
June–July											
+	3	1	1	3	0	1	3	0	5	7	0
÷	3	5	2	5	1	3	3	2	8	13	3

vival was determined by the feeding conditions and by the condition of the larvae. The feeding conditions were influenced by the number of nauplii of *Calanus finmarchicus* in May, but this dependency was not expressed very clearly. In June—July she found a negative correlation between the biomass of plankton and survival and number of cod larvae, therefore she concluded that the plankton had been consumed by the cod larvae.

The relationship between cod larvae and plankton biomass at Skrova, Eggum and Skarsvåg—Ingøy in 1949—1972 is shown in Table 5. As observations on zooplankton are missing for a number of years no conclusions may be drawn with certainty. As mentioned by Sysoeva (1973) eggs and larvae of copepods (*Calanus finmarchicus*) which are important as food for cod larvae, may be abundant in April—May, even if the biomass of zooplankton is small. It may therefore be concluded that it is the *quality* and *particle size* rather than the quantity of zooplankton which is the critical factor for the survival of the cod larvae.

The relationship between the size of the year classes and the abundance of cod larvae is shown in Table 6. For the poor year classes a positive correlation seems to exist with a low abundance of cod larvae both in

Table 6. Number of cases with high (+) or low (—) abundance of cod larvae along the coast of northern Norway in April–June and June–July and the same year-classes 2 + years old. Data from Table 2.

Year-class	Abundance of cod larvae			
	April–June		June–July	
	+	—	+	—
Rich	3	3	2	1
Medium	6	2	1	2
Poor	2	8	1	5

April—June and June—July, for the rich and medium year classes combined, a positive correlation in April—June. The observations are, however, too few to be reliable. Wiborg (1957) found no correlation between abundance of cod eggs and larvae in the Lofoten area and the size of the corresponding year classes.

CONCLUSION

It may be concluded that plankton observations from single stations close to the Norwegian coast mainly reflect the local conditions. When plankton hauls are taken at long time intervals, occasional patchiness may obscure the variations. This is especially felt for the quantitative observations.

Continuous observations during a series of years may nevertheless yield valuable information on the general trends in the development and quantity of the plankton, especially when combined with information from other sources on physical, chemical and biological parameters.

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Table I. Plankton displacement volumes per m² of sea surface at the permanent oceanographical stations along the coast of Norway and at St. M in the Norwegian Sea during the years 1949- 1972. Mean of the monthly averages and mean of the months April—August of the different years. x̄)mean, s) standard deviation, n) number of years. As the period April– August during some years is incomplete, the corresponding *n* may be larger than n̄ of the individual months, see text, p 468.

	J	F	M	A	M	J	J	A	S	O	N	D	April — August
Utsira 200-0 m (1976—1972)													
x̄	8.1	7.8	10.0	17.6	28.1	29.4	33.2	14.8	11.3	12.4	8.7	4.0	26.3
s	5.90	3.98	7.70	8.56	18.45	15.59	25.47	4.52	6.01	7.26	8.79	3.17	13.77
n	5	5	4	6	5	5	6	5	5	5	5	5	6
Utsira 50-0 m (1967—1972)													
x̄	3.2	2.9	8.3	12.9	18.5	20.3	15.0	5.8	7.6	5.4	3.4	1.5	17.0,
s	2.14	1.25	6.43	7.16	16.65	12.70	12.21	1.80	8.40	4.50	4.27	0.97	7.39
n	5	5	4	6	6	5	6	5	5	5	5	5	5
Sognesjøen 200-0 m (1949—1962)													
x̄	1.2	2.2	2.2	10.3	8.5	7.9	7.4	3.9	6.1	2.4	1.7	1.1	7.7
s	0.67	1.51	1.78	6.96	8.35	3.89	8.12	2.83	6.64	1.12	0.95	0.51	2.93
n	6	6	11	11	10	10	10	9	8	10	8	7	13
Sognesjøen 200-0 m (1963—1972)													
x̄	3.5	3.0	12.0	17.8	26.1	12.3	8.8	12.0	8.5	8.7	4.1	5.1	17.4
s	2.71	2.75	10.22	10.78	14.20	6.46	5.24	3.85	4.94	8.25	2.00	5.90	7.64
n	9	6	9	10	10	7	9	10	8	7	6	7	10
Sognesjøen 50-0 m 1949—1962)													
x̄	0.4	0.4	2.3	6.2	5.4	7.3	3.6	3.5	4.1	1.6	0.8	0.4	5.1
s	0.34	0.37	1.3	3.58	5.48	3.90	1.58	3.55	7.67	1.33	0.95	0.31	1.45
n	9	6	9	10	10	10	8	7	8	9	8	8	11

Sognesjøen 50-0 m (1963—1972)

$\bar{x}$	2.8	3.3	8.2	14.4	26.6	9.0	7.4	10.5	4.5	7.5	4.2	2.0	14.5
s	0.65	2.40	3.61	15.30	15.79	8.24	4.42	6.86	2.21	12.98	2.50	1.14	5.91
n	9	6	8	10	10	6	9	10	7	7	8	9	10

Ona 200-0 m (1949—1953)

$\bar{x}$	1.5	1.5	3.8	12.3	12.2	15.7	31.3	5.2	2.7	2.8	2.6	1.7	15.3
s	1.07	0.35	2.53	6.37	7.37	8.54	20.17	3.42	1.76	1.04	1.39	1.63	4.10
n	3	3	3	5	5	3	5	5	5	5	4	2	5

Ona 50-0 m (1949—1953)

$\bar{x}$	—	1.0	2.3	5.3	8.6	7.0	1.9	0.8	2.1	1.1	3.0	1.1	4.7
s		0	0	3.51	8.80	4.60	2.02	0.29	1.93	0.64	0	0	3.36
n		1	1	4	4	3	3	3	3	2	1	1	4

Skrova 300-0 m (1949—1962)

$\bar{x}$	12.0	9.7	7.9	12.3	24.5	25.7	22.1	23.7	16.0	16.2	13.6	13.9	21.8
s	4.23	3.82	3.25	4.35	8.87	8.35	9.52	19.75	7.71	7.48	4.53	4.54	7.65
n	12	11	11	11	13	13	14	14	14	12	11	13	14

Skrova 300-0 m (1963—1972)

$\bar{x}$	22.9	15.8	17.4	17.2	30.8	43.1	50.4	33.0	32.4	36.4	28.6	23.3	34.9
s	6.71	6.04	9.75	4.78	11.00	17.38	22.83	15.61	17.26	15.21	18.01	13.07	18.35
n	10	10	10	10	10	10	10	10	10	10	9	6	10

Eggum 200-0 m (1949—1962)

$\bar{x}$	1.7	1.4	1.52	8.9	52.5	41.7	47.9	15.3	9.8	8.9	4.9	3.8	32.0
s	1.17	1.17	1.06	6.74	40.37	28.12	40.62	9.04	6.66	4.07	3.86	2.33	19.24
n	8	6	6	9	7	10	8	9	8	7	6	6	9

Eggum 200-0 m (1963—1972)

$\bar{x}$	5.3	6.6	6.9	22.0	61.8	58.8	67.0	44.9	32.1	7.0	6.8	7.4	54.1
s	4.10	5.09	7.66	12.49	56.44	25.02	22.17	25.67	25.37	9.97	4.41	5.98	16.74
n	5	2	4	3	9	8	8	7	7	6	7	5	8

	J	F	M	A	M	J	J	A	S	O	N	D	April – August
Eggum 50-0 m (1949–1962)													
$\bar{x}$	0.6	0.6	0.9	3.1	33.5	14.0	6.8	4.9	2.3	3.1	1.6	0.8	11.9
s	0.6	0.76	0.94	2.63	41.30	11.43	8.68	4.76	1.55	2.40	1.91	0.76	9.38
n	7	6	5	7	7	10	9	7	9	7	5	6	9
Eggum 50-0 m (1963–1970)													
$\bar{x}$	2.3	3.0	5.6	12.5	42.6	42.7	35.8	13.9	16.0	11.9	2.3	3.2	30.8
s	1.27	0	2.40	6.45	39.79	26.32	18.29	7.39	21.50	16.10	1.94	2.14	13.61
n	3	2	3	4	8	7	8	8	8	8	7	4	8
Skarsvåg 260-0 m (1955–1962)													
$\bar{x}$	2.9	2.1	2.7	3.1	11.5	26.6	31.3	19.0	18.1	7.5	6.7	8.0	19.5
s	0	1.00	1.37	1.46	6.99	20.61	28.79	13.95	9.65	1.98	4.18	4.19	13.14
n	2	3	4	6	7	7	8	8	8	6	8	4	8
Skarsvåg 260-0 m (1963–1966)													
$\bar{x}$	8.6	4.0	5.4	4.5	22.5	39.5	45.5	22.5	24.0	28.0	7.5	1.8	30.7
s	5.89	2.11	4.82	2.12	19.08	15.86	42.00	19.36	13.08	15.10	2.12	0	16.10
n	3	3	4	2	4	4	4	4	3	3	2	1	5
Skarsvåg 50-0 m (1955–1962)													
$\bar{x}$	0.5	10.0	10.0	2.4	5.7	11.1	14.9	6.2	3.9	2.7	2.0	2.2	9.6
s	0	0	0	0.78	3.79	7.11	12.83	3.76	2.45	2.15	1.41	1.42	6.0
n	2	1	1	2	5	6	8	8	5	5	2	4	8
Skarsvåg 50-0 m (1963–1966)													
$\bar{x}$	4.0	3.0	3.0	7.5	9.0	14.7	16.5	9.8	11.7	5.6	3.0	3.0	12.1
s	1.73	0	0	6.36	4.24	5.29	7.14	2.87	10.92	2.42	0	0	2.66
n	3	4	4	2	4	4	4	4	4	3	1	1	4

Ingøy 50-0 m (1969—1972)

$\bar{x}$	1.9	1.8	1.6	2.4	18.7	26.7	56.3	13.6	5.4	2.4	2.0	2.4	23.1
s	1.85	1.11	1.13	1.60	10.13	10.50	37.88	7.27	3.29	2.26	2.26	1.13	9.67
n	3	3	2	3	3	4	3	4	4	2	2	2	4

Ingøy 300-0 m (1969—1972)

$\bar{x}$	10.4	4.0	4.8	5.3	30.9	50.7	80.2	26.2	22.2	7.6	12.5	8.0	39.2
s	4.45	3.70	5.66	3.33	12.76	17.39	75.18	10.58	21.00	9.62	8.17	3.39	16.80
n	3	4	2	3	3	3	3	4	4	2	3	2	4

St. M 100-0 m (1950—1965)

$\bar{x}$	0.6	0.7	4.0	8.2	12.6	19.0	16.6	10.2	4.3	3.7	2.1	1.2	13.3
s	0.46	0.40	2.10	5.33	4.71	13.46	6.91	6.25	2.44	2.22	1.35	1.15	6.31
n	13	14	13	14	15	15	12	10	11	9	9	9	16

St. M 100-0 m (1966—1972)

$\bar{x}$	2.5	2.0	7.5	15.8	28.0	30.2	29.1	23.8	12.2	5.0	3.6	18.0	27.1
s	3.06	0.98	8.18	8.49	20.44	19.53	19.78	15.65	11.10	3.50	3.94	0.93	5.99
n	7	7	9	9	9	9	5	5	5	5	5	5	7

St. M 600-0 m (1950—1965)

$\bar{x}$	11.9	13.9	24.8	28.1	30.9	35.9	37.0	30.3	21.8	21.2	14.6	14.9	31.5
s	4.60	5.65	11.75	13.23	17.83	20.62	25.76	13.07	7.20	9.45	4.15	10.81	13.79
n	11	11	12	14	15	16	12	10	11	8	8	8	16

St. M 600-0 m (1966—1972)

$\bar{x}$	20.0	26.1	43.6	69.2	58.4	57.7	52.4	52.9	40.3	38.1	22.2	15.3	61.8
s	7.87	7.47	16.57	24.76	24.51	23.15	30.94	15.67	13.37	15.42	6.81	9.41	6.77
n	7	7	7	7	7	7	7	5	5	5	5	5	7

FiskDir. Skr. Ser. HavUnders., *16*: 489—505.

PHYTOPLANKTON OBSERVATIONS IN OFFSHORE NORWEGIAN COASTAL WATERS BETWEEN 62°N AND 69°N

I. Variation in time of the spring diatom maximum 1968—71

By

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ABSTRACT

Braarud, T. and Nygaard, I. 1978. Phytoplankton observations in offshore Norwegian coastal waters between 62° N and 69° N. I. Variation in time of the spring diatom maximum 1968—71. *FiskDir. Skr. Ser. HavUnders.*, *16:* 489—505.

An attempt was made to trace yearly fluctuations in the timing of the spring diatom maximum along the Norwegian west coast, 62° N—69° N. Quantitative data on the diatom population at 281 stations with 0 m samples and 120 stations with additional samples from the 10, 20 and 30 m levels, collected in March—April during the four years 1968—71, were used. A delay of about three weeks from the southern to the northern part of the area, as previously observed, was again established. The years 1970 and 1971 were years with an early maximum while 1969 was a definitely late year within the whole area. The time variation in 1968—71 recorded in the Trøndelag and Helgeland subareas, showed trends different from those of the neighbour areas. The phytoplankton data were not adequate for a detailed analysis of the factors responsible for the timing of the maximum each year in the respective parts of the investigated area.

PREFACE

A study of the plankton in offshore coastal waters along the Norwegian coast from Møre to Vesterålen was adopted as part of the Norwegian contribution to the International Biological Programme (IBP), section Marine Productivity (PM). The plankton work formed an integrated part of a marine biological survey, "The recruitment mechanism for herring and cod", undertaken by the Institute of Marine Research, Fisheries Directorate, Bergen, in March—April 1968—71.

The present report on the phytoplankton material deals with the variation in time of the spring diatom maximum of the near-coastal and intermediate coastal waters off Møre, Trøndelag, Helgeland and Vestfjorden—Vesterålen in 1968—71.

Cand. real. Ingrid Nygaard carried out the microscopical examination by means of the Utermöhl technique (Utermöhl 1931) of the water samples from 400 stations. The financial support through IBP sources was, however, inadequate for her continued engagement at the project until the results could be presented for publication. The senior author is, therefore, mainly responsible for the editing of the report.

In subsequent reports, accounts will be given of the seasonal and regional occurrence of the more important diatom species and of groups playing a subordinate role in the phytoplankton during March—April.

INTRODUCTION

In Norwegian coastal waters the spring diatom maximum is the most spectacular event in the annual phytoplankton cycle as indicated by popular designations as "bloom" or "outburst". Within a period of few weeks a huge production of organic matter takes place, doubtless being of major importance for the secondary producers and the subsequent links in the production chain. Success of the reproduction of these later stages may depend upon a satisfactory coordination in time of spawning and availability of food for the fish larvae. In this connection variation in time of the season of high productivity by phytoplankton in spring may play a role.

With this reasoning in mind, a program for the study of phytoplankton in water samples collected during a survey organized by the Institute of Marine Research, Fisheries Directorate, Bergen, was set up. The purpose was to bring out information on variation from year to year and from one part of the area of investigation to the other in the time of the diatom maximum.

SUBAREAS AND WATERMASSES

For the present purpose, the area of investigation was divided in four subareas (fig 1):

Møre — from 62° N to 63° 30° N
Trøndelag — from 63° 30° N to 65° N
Helgeland — from 65° N to 67° N
Vestfjorden—Vesterålen — from 67° N to 69° N

The topography and hydrography of the offshore coastal areas which the survey covers, are so diverse that the environmental situation for phytoplankton and zooplankton, even within one of the subareas, exhibits a rather broad range. In order to obtain a meaningful basis for

Fig. 1. A. The investigated area for the phytoplankton survey 1968—71 of the Norwegian IBP—PM project.

B. Number in circles: Reference to previous quantitative phytoplankton studies in spring in Norwegian offshore coastal waters north of 62° N. 1) Lopphavet, Heimdal 1974. 2) Malangen, Gaarder 1938. 3) Lofoten, Føyn 1929; Gran 1930. 4) Vesterålen, Gran 1930; Braarud *et al.* 1958. 5) Vestfjorden, Nordli 1949; Braarud *et al.* 1958. 6) Møre, Gran 1929, 1930; Braarud and Klem 1931.

comparison of the time sequence of the spring diatom development along the coast, a division of the watermasses encountered in a section from a fjord area out to the atlantic drift has been adopted for the upper 50 m. In addition to the old distinction between coastal and atlantic water based on salinities (Helland-Hansen and Nansen 1909), the term "semi-atlantic waters" for stratified waters with coastal water overlying Atlantic water within the upper 0—50 m layer is introduced. This situation may be expected to involve a certain admixture of atlantic water to the overlying water within the euphotic zone. Trophic conditions for phytoplankton growth may in the semi-atlantic waters differ essentially

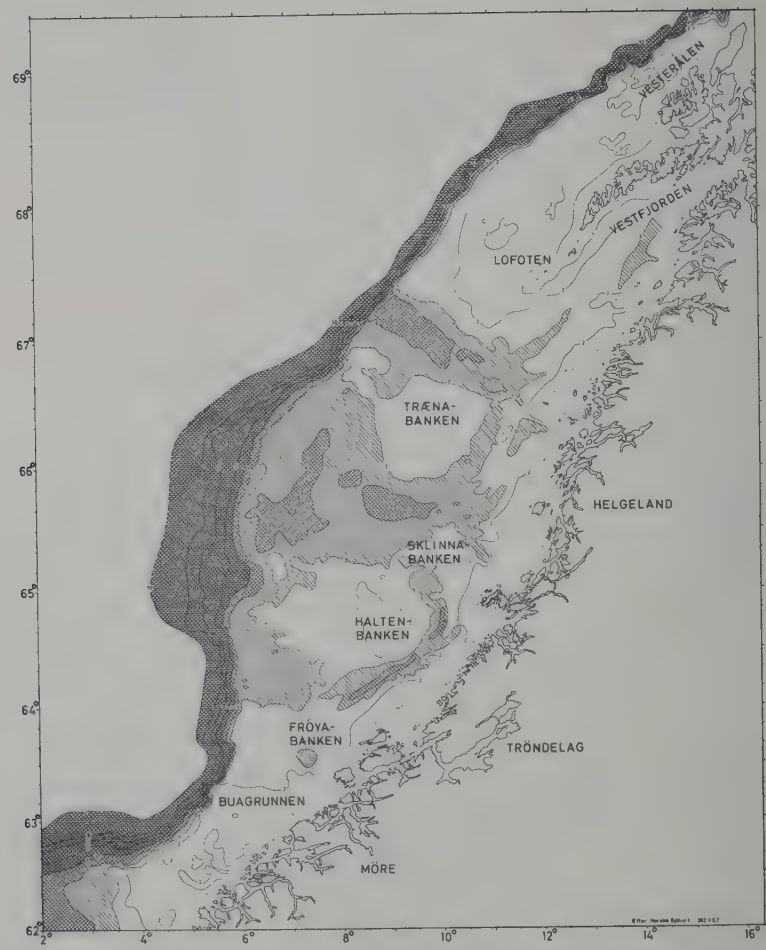

Fig. 2. Bathymetric map of the investigated area. Depths in hectometer. The figure represents an extension of Fig. 1 in NAKKEN and LJØEN (1969) and was supplied by LJØEN.

from those in the coastal waters, and the same may pertain to other environmental conditions as well. In Fig. 3 a diagram is shown, indicating the five categories of watermasses encountered in the section. While the border lines between the atlantic and semi-atlantic waters and between the latter category and the intermediate coastal waters are based upon

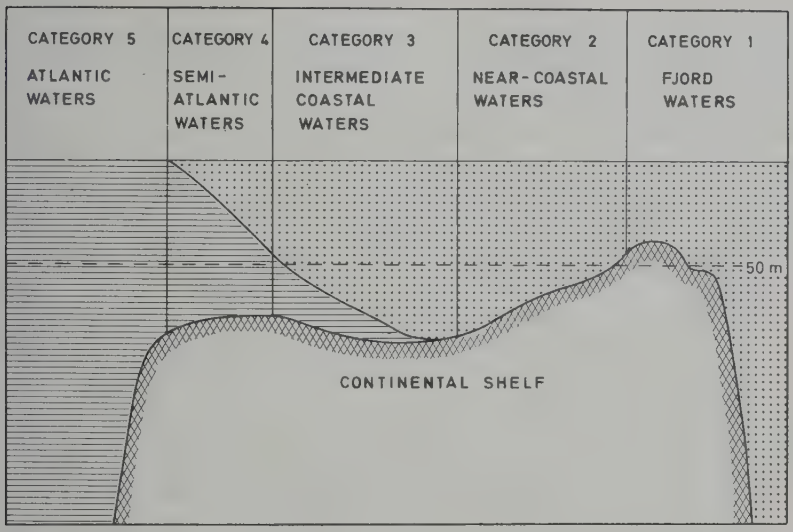

Fig. 3. A hydro-topographical division of the watermasses 0—50 m on the Norwegian west coast. Salinities within the 0—50 m layer: Category 1, 2 and 3) lower than 35‰, category 4) lower than 35 ‰ in the uppermost strata, higher than 35‰ beneath, category 5) higher than 35‰, even at the surface. ≡ >35‰, ⁙ <35‰

hydrographical criteria, the topographical delineation of the intermediate coastal and the near-coastal waters is more arbitrary. The extention of the various categories differs with locality and season, and may show yearly variation within any of the subareas investigated.

QUANTITATIVE PHYTOPLANKTON DATA 1968—71

At most of the stations surface samples only were examined while in some cases samples from the 10, 20 and 30 m levels were also studied. In Table 1 the number of stations of the two categories are given for the four subareas and for each year. Only 2 ml samples were examined, using the Utermöhl technique. Original tables for each station as well as excerpt tables for the various cruises are deposited at the University of Oslo, Department of Marine Biology and Limnology. Hydrographical data are available from the Norwegian Oceanographic Data Centre, Bergen.

The situation in semi-atlantic and atlantic waters will be considered in a subsequent report.

Table 1. Stations for which quantitative phytoplankton data were obtained. Italized figures indicate numbers of stations with data for more than the 0 m sample. Otherwise only the 0 m sample has been examined. The number of stations of each category as well as their total number are given for each subarea and each year.

Year	Area				Sum for each year
	Møre	Trøndelag	Helgeland	Vestfjorden —Vesterålen	
1968.....	56 + *5*	20 + *7*	11 + *3*	26 + *11*	113 + *26*
1969.....	16 + *5*	7 + *5*	17 + *3*	29 + *8*	69 + *21*
1970.....	14 + *9*	21 + *17*	7 + *15*	15 + *13*	57 + *54*
1971.....	6 + *2*	21 + *2*	3	12 + *15*	42 + *19*
	92 + *21*	69 + *31*	38 + *21*	82 + *47*	281 + *120*
Sum for each subarea.	113	100	59	129	Total 401

METHOD FOR ESTIMATING THE TIME OF THE SPRING DIATOM MAXIMUM

In handling the observational data, which are scattered in time as well as geographically, it was found neccessary to refer the situation at each station to a common scale, indicating various stages of the spring diatom increase. It is obvious that the adoption of such a procedure for the whole area of investigation requires that it is not based upon too strict a gradation. Conditions in the Møre area in the south and in the Vestfjorden—Vesterålen area in the north are so different hydrographically (Braarud, Gaarder and Nordli 1958) that it might have been preferable to treat them separately. However, the inclusion of the two subareas in the middle of the coastal region investigated, makes it infeasible to draw any rational division line between a southern and a northern situation. We shall, therefore, deal with each of the four subareas shown in Fig. 1.

The following stages of the spring diatom increase were distinguished:

Stage 0 — No sign of any increase of the diatom population after the winter minimum.
— I — A definite increase is noticeable.
— II — The diatom population has reached about 50/ml.
— III — The diatom population has increased further, apparently approaching maximum.
— IV — The population has reached 1 000/ml or more.
— V — Post-maximum situations are given this designation, regardless of the size of the diatom population.

This coarse scale is subjective, and other criteria than the numerical size of the diatom population have been employed as well. A sample with a diatom population of 100/ml might either be referred to stage III or to V. The additional criteria which then have been considered are: 1) The composition of the diatom community, 2) the occurrence of resting stages and, in some cases, the general composition of the other components of the phytoplankton.

When the composition of the diatom population is used, our knowledge from previous investigations of the spring diatom increase has been employed, such as the early appearance of *Chaetoceros socialis* and *C. furcellatus*. The percentage of resting spores in these species is also taken as an indicative detail.

During the collation of the phytoplankton data from this survey, observations were made on the relative abundance of the artificial group "monads and unidentified flagellates" (MF) at various stages of the diatom spring growth. In the south a definite increase took place after the diatom maximum had passed. A detailed discussion of the quantitative distribution pattern of this group relative to the diatom population is planned to be published separately. For the Møre area in 1968, when the observational material was relatively adequate, a condensed table is presented (Table 2). It indicates that post-maximum stages are apt to have acquired much larger populations of MF than those occurring in pre-maximum stages with similar diatom abundance or when the diatom maximum is reached. In the northernmost area, the picture is not as consistent in this respect, possibly because density stratification at this time of the year is far less pronounced in the northern than in the southern area (Braarud *et al.* 1958).

Table 2. Changes in the component "Monads and unidentified flagellates" (MF) during the phytoplankton development in the offshore coastal waters after the winter minimum. Examples from the Møre area in 1968. Populations as cells/ml. For definition of development stages 0—V, see p. 494.

Stages	0	I	II	III	IV	V
Cruise 2a						
7—12 March						
Number of stations	9	—	—	—	—	—
Diatoms, cells/ml	<8					
MF, cells/ml						
Range.....	3—23					
Mean.....	10					

Table 2 cont.

Stages	0	I	II	III	IV	V
Cruise 2b						
25—27 March						
Number of stations	—	—	3	2	7	—
Diatoms, cells/ml	—	—	<250	<800	2300–5800	—
MF, cells/ml						
Range			7—14	1—22	1—21	—
Mean.....			10	11	9	
Cruise 3a						
7—8 April						
Number of stations	2	3	1	5	4	5
Diatoms, cells/ml	<7	130	530	1400–1700	2600–3200	150–1100
MF, cells/ml						
Range	6—16	0—8	5	8—36	4—11	9—40
Mean.....	11	3		18	7	21
Cruise 3b						
18—23 April						
Number of stations	—	—	—	—	1	29
Diatoms, cells/ml					3800	<1—557
MF, cells/ml						
Range					11	78—3300
Mean.....						734
Cruise 4						
17—29 April						
Number of stations	—	—	—	—	2	23
Diatoms, cells/ml					1000—2500	2—481
MF, cells/ml						
Range					9—39	21—1735
Mean.....					24	574

Stage V is even less well-defined than the earlier stages. In some cases the decline of the population after the diatom maximum may be very rapid, as shown by the observations by Gran (1927) in Fig. 4. However, dependent upon the hydrographic situation and the grazing intensity, a slower decrease may occur. This may particularly be expected in the northern coastal area where wind-generated turbulence is apt to be especially effective in supplying nutrients from deeper layers to the euphotic zone due to the small density gradients encountered there at the season in question (Heimdal 1974).

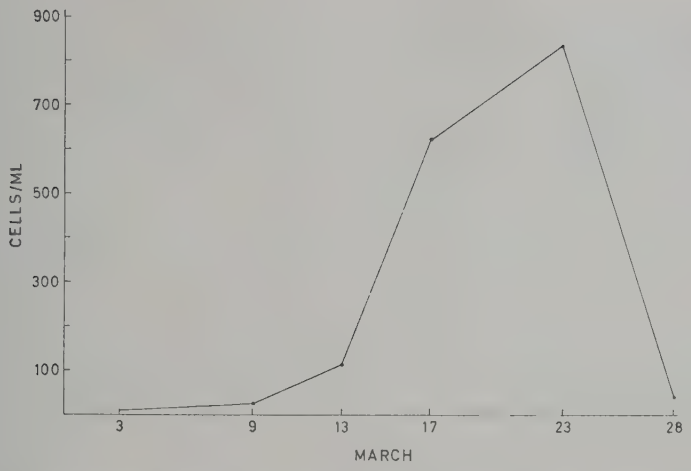

Fig. 4. Changes in the diatom population (1—2 m) at Kårtveit, south of Bergen, 3—28 March 1922. Records from GRAN (1927).

The size of the MF populations recorded may to some extent be influenced by the amount of larger forms in the sample. When diatoms are very abundant, the accuracy of the counting of the very small forms of MF is apt to be considerably reduced. For this reason the records of MF populations for stages III and IV may be too small. This inaccuracy would, however, hardly invalidate the use of the present criterion for distinguishing between stage V and stages I and II in cases when the diatom population of the former is of a similar, fairly modest size as in I and II.

VARIATION IN TIME OF THE SPRING DIATOM MAXIMUM 1968—71

The present survey can only give fragmentary information on variation in the time schedule of the spring diatom increase within the coastal area 62°—69° N. Irregularities in the cruise program of the co-operative project, curtailment of the microscopical work for financial reasons and the preselection of samples for the phytoplankton studies have made the observations less suited for a description of the time schedule in the four subareas in each of the four years of investigation.

In Table 1 the number of stations for which phytoplankton data were obtained, is given for the various years and subareas. A further documentation of the observational material on which the estimation of the time of the diatom maximum has been based, is given in Table 3 for the Møre, Trøndelag and Helgeland subareas and in Table 4 for Vest-

fjorden—Vesterålen. For each of the subareas the tables give information on which stages have been observed in each week and, for each stage, the number of stations at which it was represented is noted in parenthesis.

Fig. 5 gives a diagrammatic summary of the results. It should be accepted with due reserve since in many cases the observations are too scanty for a more accurate estimate. This is especially the case for Helgeland.

A comparison between the results for the Møre and Vestfjorden—Vesterålen subareas shows that in all years a delay in the north of 3—4

Table 3. Subareas Møre, Trøndelag and Helgeland. Summary for each year of recordings of she stages 0-V (see p. 494) observed in March-April and the first week of May. For each stage, the number of stations at which it was observed in the week and year in question is given in parenthesis.

Month	March				April				May
Week	1	2	3	4	1	2	3	4	1
1968		MØRE							
Cruise 2a, 2b, 3a, 3b, 4.....		0 (7)		III (1) IV (7)	II (1) III (2) IV (3) V (6)		V (13)		
1969 Cruise 6a, 6b, 6d					II (4) III (2) IV (2)		V (6)		
1970 Cruise 8a, 8b, 8c, 9a, 9b ...					V (3)	V (11)	V (5)	V (4)	
1971 Cruise 10		0 (4)			V (4)				
1968		TRØNDELAG							
Cruise 2a, 3a, 3b, 4		0 (1)			III (2)		V (3)	V (13)	V (1)

Table 3 cont.

Month	March				April				May
Week	1	2	3	4	1	2	3	4	1
1969 Cruise 6a, 6c, 6e					II (5)		V (2)		V (1)
1970 Cruise (8a, 8b) 9a, 9b					V (5)	V (8)		V (10)	
1971 Cruise 10	0 (15)				V (9)				
1968 Cruise 3a, 3b, 4	HELGELAND				0 (1) I (2)		V (5)	V (3)	
1969 Cruise 6b, 6c, 6d, 6e						0 (1) I (1)	II (6)	V (3)	V (5)
1970 Cruise 8a, 8b, 9a, 9b					0 (2) I (2) II (1)	0 (2) I (1) II (2)		V (4)	
1971 Cruise 10				0 (2)	0 (2)				

weeks was registered. This is in accordance with previous investigations in these areas (see p. 491). An earlier spring maximum in Vestfjorden than in near-coastal waters off Vesterålen, which was indicated in 1968—71, has also been observed before. The early stages of the diatom increase in these areas were, however, rather synchronous.

The two subareas between Møre and Vestfjorden do not seem to show any consistent agreement with the trend of the yearly variation of any of their neighbour areas during the four year period. For Møre and Trøndelag, there was in 1968 and 1969 a considerable time difference

Table 4. Vestfjorden—Vesterålen. The various stages of the spring diatom development late March to early May, 1968 1971. Scale 0—V, see p. 494. For each reference to stage the number of stations is given in parenthesis. See also legend to Table 3.

		Vestfjorden, outer and central						Offshore					
Month		March	April				May	March	April				May
Week		4	1	2	3	4	1	4	1	2	3	4	1
	Central	I—II				V		Near	II			V	
1968		(4)				(5)		the coast	(1)			(8)	
Cruise													
1a, 1b	Outer	I—II				IV		Farther	I			IV	
		(4)				(5)		offshore	(8)			(3)	
				0									
				(1)									
1969	Central			I		V		Near the			I	V	
Cruise				(2)		(8)		coast			(2)	(5)	
5a, 5b				II									
				(2)									
	Outer			I—II			V	Farther			0	V	
				(7)			(3)	offshore			(5)	(2)	
	Near			IV				Near the			II—		
1970	land			(1)				coast			III	V	
Cruise											(6)	(3)	
7a, 7b	Outer			II			V	Farther			0—I	V	
				(3)			(5)	offshore			(3)	(3)	
	Central		II				V	Near the	0—				IV—
1971			(5)				(3)	coast	II				V
Cruise									(2)				(2)
11a,	Outer		II				IV—	Farther	0				IV—
11b			(3)				V	offshore	(4)				V
							(1)						(5)

while in the «early years» 1970 and 1971 the maxima appeared to be synchronous. With regard to the time variation from year to year, the situation in the four subareas cannot be expected to have the same trend considering the large geographical distance which they cover. However, an earlier maximum in Vestfjorden in 1970 and 1971 than in the other years is in accordance with what was observed in Møre and Trøndelag.

COMPARISON WITH RESULTS FROM PREVIOUS SURVEYS

For the Vestfjorden—Vesterålen area observations are available for a number of years. On the basis of these, we have tried to give a characterization of the various years by reference to the scale which has been

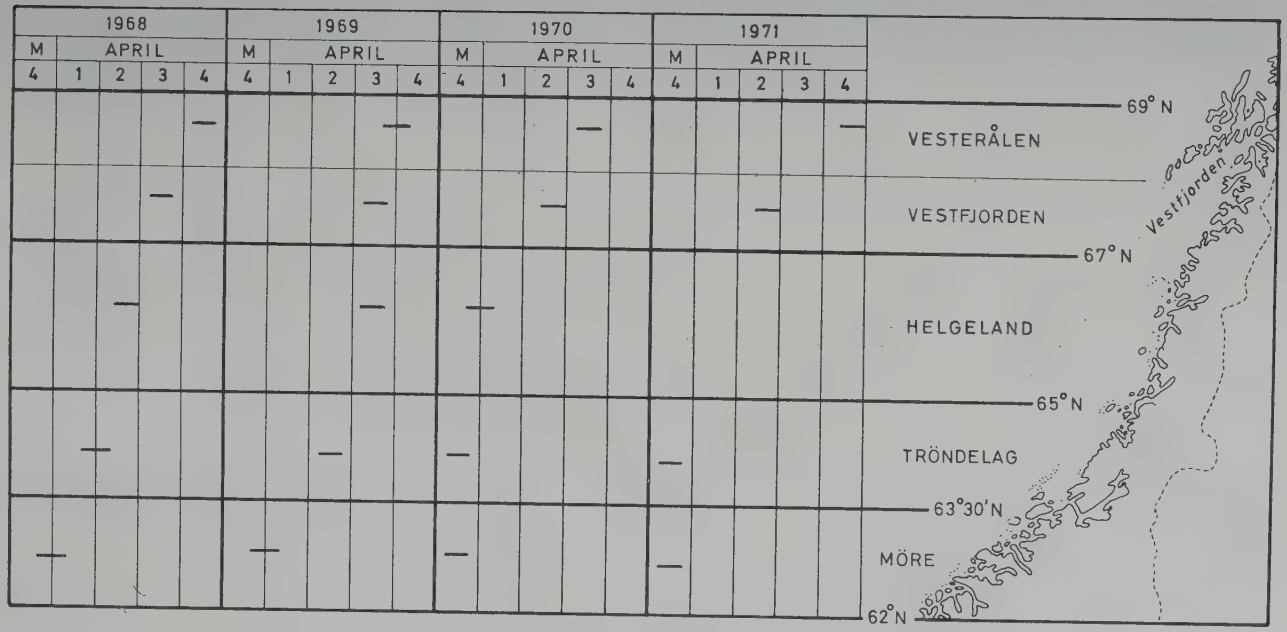

Fig. 5. Estimated occurrence of the spring diatom maximum in four subareas of the Norwegian coast between 62° N and 69° N in 1968, 1969, 1970 and 1971. The diagram is based upon observations in the near-coastal waters, and the time is indicated by weeks, from the fourth week of March to the fourth week of April. For data and methods, see the text.

Table 5. For the period 3rd week of March to 2nd week of May, available quantitative phytoplankton data have been used for a characterization of the spring diatom development with the use of a 0—V scale (see p. 494) and reference to the nearest week. The origin of the data is given in the text. The Malangen locality is not strictly offshore, but at the mouth of a fjord system, while the station on the shelf off Ullsfjord is comparable to the near-coastal stations in Vesterålen.

A	Vestfjorden										Offshore on the shelf									
Month	March		April				May				March		April				May			
Week	3	4	1	2	3	4	1	2			3	4	1	2	3	4	1	2		
1922		0	I—II	II		II														
1923	0	0	0—II	II	II	II—								I—						
					III	V								IV						
1924	0	0	I	I—II								0		I						
1925							V													
1926		0—I	I	I	II	V		V				0	I	III		V			V	
1927						V										V				
1929	0	0	0	I	0—II	V						0				IV				
1945		II		III		V							I			V				
1946	I											I		II		V				
1949[1])														IV						

B	Malangen 1930—31								The shelf off Ullsfjord (U 3) 1963—64									
	I				IV	V		V		0		I				I		

[1]) Observation from a single station by NORDLI (1949).

used for 1968—71, defined on p.494. The results are presented in Table 5 A, based on observations in 1922—27 by FØYN (1929), in 1929 by GRAN (1930) and in 1945—46 by BRAARUD *et al.* (1958). As a supplement, corresponding information is given in Table 5 B for Malangen and the shelf outside Ullsfjord, based on the observations by GAARDER (1938) and HEIMDAL (1974).

The following conclusions may be suggested with regard to the timing of the spring diatom development in the different years as indicated by these surveys.

In Vestfjorden — A very late maximum in 1922.
A remarkably late start of the increase in 1929.

Offshore — Somewhat early development in 1923, 1926, 1949. Late maximum in 1929.

Malangen — The situation in 1930—31 was comparable to what had been recorded in some years in Vestfjorden, perhaps with a slightly earlier maximum.

Off Ullsfjord — 1962—63, 1964. Maximum even later than in Vesterålen.

The general impression gained from these observations is that in the Vestfjorden—Vesterålen area and still further north, considerable variation may be expected from one year to another as to the time when diatom growth starts after the winter minimum and the further increase towards maximum. Ordinarily the increase appears to start in the first week of April, and the maximum may, with few exceptions, be observed in the third to fourth week of April. However, deviations from this time schedule seem well documented in the publications mentioned above.

From the other subareas the only observations which may be used for comparison with the results from the present survey, are those by Gran (1929, 1930) from Møre.

On the basis of his quantitative investigations in 1926 and 1927 and older qualitative phytoplankton data, Gran (1929, p. 49) stated: "We found the maximum number in the Skagerrak from February—March, off Bergen during the later half of March, at Romsdalen at the end of March and during the early half of April, and at the Lofoten Islands during the first half of April." Observations from 1929 in the same section from Romsdalsfjorden to Storegga (Gran 1930) indicated that maximum had been reached in the last week of March at the stations nearest land, in agreement with his general statement quoted above.

A combination of the results from the older surveys with those from the 1968—71 survey seems to justify the following broad conclusions.

1. There is a delay of about three weeks in the occurrence of the spring diatom maximum when going from Møre (62° N) to Vestfjorden—Vesterålen (69° N). This is in accordance with the general statement by Gran (1929) quoted above as well as with observations in 1945—46 by Braarud *et al.* (1958) at Eggum and Skrova in the north and Sognesjøen and Utsira in the south.
2. In the Møre subarea, the years 1970 and 1971 had earlier maxima than 1968 and 1969 which showed a delay also compared with Gran's observations in 1929.
3. Also for the other subareas there was in 1970 a relatively early maximum, as in the Møre area, while in 1969 the maximum was relatively late in all subareas. North of Møre the variation in the time schedule in 1968 and 1971 did not show any common trend for the three subareas.
4. In the Vestfjorden—Vesterålen subarea there is generally an earlier maximum in Vestfjorden than in Vesterålen, in accordance with observations in previous surveys.

CONCLUDING REMARKS

From quantitative phytoplankton data for Eggum and Skrova in the Vestfjorden—Vesterålen area and Sognesjøen and Utsira in the southern part of the Norwegian west coast, BRAARUD *et al.* (1958) documented a delay in 1946 of about three weeks in the spring diatom development in the north compared with the south. In their summary (p. 41) they commented on the background for this delay: "Factors of general nature: the different light supply due to geographical position and the delayed vernal stabilization at the northern stations, conditioned by a smaller fresh-water supply, were pointed out as main factors causing the delay in spring phytoplankton growth in the north. Extensive winter mixing, inducing a more pronounced dilution of the winter population in the north, may also result in smaller phytoplankton stocks in early spring".

The observations from the present survey demonstrate that within the coastal area from 62° N to 69° N yearly fluctuations in the timing of the spring diatom maximum occur. They are well within the time range indicated by the general statements of GRAN (1929) and BRAARUD *et al.* (1958). In actual situations, however, the variation from year to year may be large enough to be taken into consideration in the search of causes for unsuccessful reproduction in commercial fishes. The present phytoplankton material is, unfortunately, inadequate for an analysis of the background for the yearly variations observed in the four year period 1968—71. For this purpose a concentrated study of the situation within a much smaller area would have been preferable. The hydrography of the offshore coastal waters is so complex that a very dense station net is needed for an adequate analysis of the environmental situation for diatom growth.

In a subsequent report, the variations in the composition of the diatom vegetation within the area of investigation will be discussed, also in view of the hydrographical heterogeneity of the Norwegian coastal waters (BRAARUD and NYGAARD, in prep.).

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GROWTH AND SURVIVAL STUDIES ON 0-GROUP PLAICE (*PLEURONECTES PLATESSA* L.) IN A SMALL BASIN WITH A CLOSED ECOSYSTEM

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ABSTRACT

Øiestad, V., Iversen, S. A. and Danielssen, D. S. 1978. Growth and survival studies on 0-group plaice (*Pleuronectes platessa* L.) in a small basin with a closed ecosystem. *FiskDir. Skr. Ser. HavUnders.*, *16*: 507—518.

A growth and survival experiment on 0-group plaice was carried out in a small basin during the summer of 1976. The volume of the basin was about 25 m^3, and the seawater was left stagnant during the summer. Of the initial 200 metamorphosed fry released, 154 survived, and a mean daily length increment of 0.28 mm was observed for a period of 105 days. The temperature was about 20 °C for half of the experimental period.

The main energy flow is supposed to have followed this simplified route: phytoplankton → *Mytilus edulis* produced faeces → detritus-eating crustaceae → plaice fry. Calculations of food intake and gross growth efficiency have been carried out, applying the metabolic values earlier reported (Edwards, Finlayson and Steele 1969), and the present data have been compared with their results. The basin appeared to be an ecosystem with a high production, giving better survival and growth than previous tank experiments.

In spite of the extreme temperature during midsummer, the growth was comparable to that observed under natural conditions (Loch Ewe), but the survival was far better due to lack of predators in the basin.

INTRODUCTION

In the middle of the 1960's studies on the ecology of 0-group plaice (*Pleuronectes platessa* L.) was carried out in Loch Ewe, Scotland (Edwards and Steele 1968, Steele and Edwards 1970). In order to interpret the observations, a number of experiments with 0-group plaice and their main prey organism, *Tellina tenuis* (L.), in the lake was undertaken at Aberdeen in laboratory tanks (Edwards, Finlayson and

Steele 1969, Edwards, Steele and Trevallion 1970), in large outdoor tanks (Edwards *et al.* 1970) and in underwater tanks (Steele 1966).

They made estimates of the metabolism and the Q_{10}, which were used to calculate the carrying capacity of Loch Ewe and to explain the observed fish growth in relation to the feeding conditions.

The main conclusions drawn from their field and laboratory investigations were:

1. Predation was the main controlling factor for the size of the population of 0-group plaice, permitting better growth of the surviving fry due to lesser competition.
2. There seemed to be a maximum gross growth efficiency of 40%.
3. The metabolism was modified by the food supply.

The experiment on 0-group plaice described in this paper was carried out to study growth and survival in a stagnant outdoor basin where the growth of the fish was limited by the carrying capacity and the high temperature of the basin water.

The experiment was carried out at Statens Biologiske Stasjon Fløde-vigen, Arendal, in southern Norway.

MATERIAL AND METHODS

On 2 March a large number of plaice eggs were fertilized and incubated in a laboratory tank. The larvae hatched about 20 March and were fed on newly hatched *Artemia salina*. The temperature increased slowly from 7 °C in March to 11 °C on 17 June when 226 metamorphosed fry were sampled randomly from the dense and slow growing population in the tank. Of these larvae, 200 were transferred to an outdoor basin while the remaining 26 were length measured.

The basin had a surface area of 18.5 m^2 and a depth of 1.3 m, giving a volume of 24 m^3. The walls were made of concrete, and the bottom consisted of equal parts of bedrock, sand and mud.

During most of the experimental period a phytoplankton bloom was in progress in the basin. The warm summer in southern Norway in 1976 resulted in an increase in both bottom and surface daytime temperatures from 17 °C on 17 June to about 23 °C two weeks later. From the end of August the temperature decreased to 13 °C at the bottom in late September. Three linear temperature functions are used in the later calculations: a linear increase from 17 °C to 20 °C (day 0—20), a steady temperature of 20 °C (day 21—60), and a linear decrease from 20 °C to 13 °C (day 61—105). Due to evaporation the salinity increased from about 34‰ to about 37‰ during the experimental period.

Previous to the initiation of this experiment the basin had just been drained after an experiment on herring larvae. It was refilled with sea water on 16 June and left stagnant for the following months until drainage on 28 September when the experiment was terminated.

In addition to the plaice fry, about 200 adult *Mytilus edulis* L. were transferred to the basin, most of them hanging in a basket at a depth of 3/4 m, but some clusters were also placed on the bottom. The *M. edulis* were intended to harvest the phytoplankton production, and their faeces would serve as food for the detritus-eating crustaceae in the basin. Two small *Carcinus maenas* (Pennant) were also released to clean the basin.

The equations used in the calculations of metabolism, growth rate, food demands and food intake are mainly taken from Edwards *et al.* (1969, 1970) and from Ware (1975). The different concepts are reviewed in the Appendix.

RESULTS

The length distributions of the larvae for the day of transfer, 17 June, a sample from 7 July and the fry surviving on 28 September are given in Fig. 1. The mean lengths on the three days were 14 mm, 23 mm and 43 mm respectively.

The intervals between the measurements were 20 and 85 days respectively, giving a daily increment of 0.49 mm for the first period, 0.23 mm for the second and 0.28 mm for the total 105 day period.

The mean weight of the fry was 23 mg on 17 June, increasing to 112 mg on 7 July, and at the end of the experiment it was 742 mg. This gives a specific daily growth rate based upon wet weight of 7.9% for the first 20 days, 2.2% for the next 85 days and 3.3% for the whole experimental period.

On 28 September a total of 154 fry had survived, giving a survival of 77% and a daily mortality rate of 0.0025.

The density of fry in the basin decreased from 11/m² to 8/m². The diet consisted mainly of harpacticoid copepods, juvenile amphipods and

Table 1. The gut contents of five plaice fry caught on 28 September (I = 3.8 cm).

Prey organisms	Occurence	Mean number per gut	Mean length of prey organisms
Amphipod juveniles	0— 20	7	3 mm
Chironomid larvae	1— 22	10	2 mm
Harpacticoid copepods (small) ...	15— 35	20	0.5 mm
Harpacticoid copepods (large) ...	135—300	210	1.3 mm

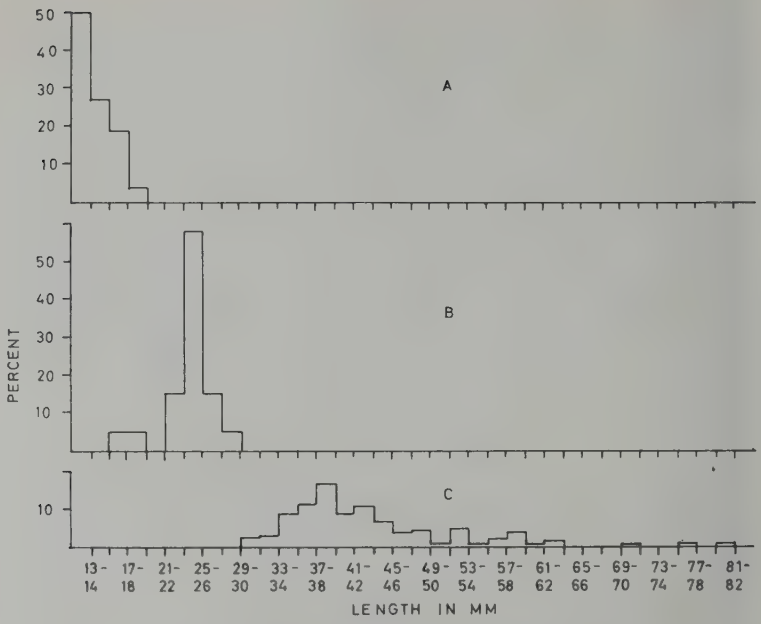


Fig. 1. Length distribution of plaice fry in the basin.
A: 17 June, B: 7 July, C: 28 September.

chironomid larvae (Table 1). The calorific value of the stomach contents on 28 September based on five fry ranged from 5 to 15 cal with a mean of 10 cal.

DISCUSSION

Steele and Edwards (1970) stated that predation was the main reason for the reduction of the standing stock of fry in Loch Ewe. They observed that mortality was negligible among fry exposed to a controlled environment without any predation compared to heavy mortality in the loch (Table 2) (Steele 1966, Edwards *et al.* 1970, Steele and Edwards 1970). The same effect was clearly demonstrated in the Flødevigen basin experiment, leading to a high survival rate.

The density of fry in Loch Ewe decreased from about 1/m² in late June to about 0.1/m² in late September. The densities were considerably higher in the tanks on land and in the underwater tanks (up to 15/m²) and were in most cases only reduced to half the initial values (Table 2).

Table 2. A comparison between different growth and survival studies on plaice fry.

	Daily mortality rate	Daily growth rate (mm)	Density/m²		Duration in days
			June	September	
Loch Ewe 1965	0.025	0.37	1.0	0.1	105*
1966	0.023	0.30	0.3	0.03	105*
1967	0.008	0.20	—	—	105*
1968	0.016	0.32	—	—	105*
Tank experiments	0.01—0.0016	0.16—0.25	15—1.5	4.1—0.9	130**
Underwater tanks	0.01—0.005	0.05—0.25	15—1.5	7.2—0.8	105***
Flødevigen experiment	0.0025	0.28	11	8	105

* Calculated for the period 17 June—28 September, data from Steele *et al.* (1970).
** Calculated for the period 5 May—15 September (the actual experimental period), data from Edwards *et al.* (1970).
*** Calculated for the period 17 June—28 September, data from Steele (1966).

The initial density in the basin experiment at Flødevigen was comparable with that of the tank experiments at Aberdeen, but the reduction in number per m² was considerably less.

Steele (1966) concluded that a density above 1.5 fry/m² would permit survival, but would lead to a reduced growth rate compared with the natural conditions.

The growth rate in the basin experiment was 0.28 mm/day during the 105 day period at a density between 11—8 fry/m². During midsummer the growth rate might have been low due to the high temperature. Therefore, the main growth probably occurred during the first and last part of the experiment as indicated by the high growth rate observed during the first 20 day period when the temperature was more favourable.

Nevertheless, the observed mean daily growth rate at Flødevigen was much higher than the observed length increment in most of the underwater tanks and even higher than in the tank with the lowest density (Table 2). The basin growth rate is, however, comparable with the growth rate under natural conditions in Loch Ewe for the same period. This was the case even though the temperature was near the lethal limit (Edwards *et al.* 1969, Edwards and Steele 1970, Danielssen and Iversen 1976), the density considerably higher, and the growth completely dependent upon production within the small basin.

The use of an enclosed system gives an opportunity to calculate the production within the system. The survival of the bottomliving animals, *M. edulis*, *C. maenas* and the plaice fry in this shallow basin, indicate that the oxygen supply was sufficient during the whole period, probably due

Table 3. Survival, growth, resting metabolism and temperature and the resulting values of daily food intake (I), gross growth efficiency (K), food intake as a percentage of body weight and the accumulated food intake for the total population and for individual fry according to the hypothesis suggested by Edwards *et al.* (1969).

Days since transfer (17 June)	Number of fry	Mean wet weight (mg)	Daily growth (mg wet weight)	Population biomass (gram wet weight)	Resting metab. cal/day	Temp. °C	First hypothesis: E = 2Q*					Second hypothesis: E ~ Q***				
							I_1	K in	$\frac{I_1 100}{W'^{**}}$	$\Sigma I_1 N$	ΣI_1	I_2	K in	$\frac{I_2 100}{W'^{**}}$	$\Sigma I_2 N$	ΣI_2
	N	W	G		Q	t	cal	%	(%)	kcal	kcal	cal	%	(%)	kcal	kcal
0	200	23	—	4.6	5.7	17.0	—	—	—	—	—	—	—	—	—	—
10	195	76	4.3	14.8	18.2	18.5	58	7.3	77	100	0.5	33	12.9	44	72	0.4
20	190	122	4.9	23.2	30.2	20.0	93	5.2	77	248	1.3	49	10.0	40	152	0.8
30	185	174	5.8	32.3	39.0	20.0	119	4.6	69	450	2.4	61	9.5	35	256	1.3
40	181	232	6.1	42.0	48.0	20.0	145	4.2	63	694	3.7	73	8.4	31	379	2.0
50	176	296	6.8	52.2	57.2	20.0	173	3.9	59	981	5.3	85	7.9	29	520	2.8
70	168	442	7.9	74.2	64.5	18.4	195	4.0	44	1,647	9.2	97	8.1	22	845	4.7
90	159	612	9.1	97.8	51.5	15.3	160	5.7	26	2,236	12.8	85	10.7	14	1,146	6.5
105	154	742	6.9	114.3	41.3	13.0	127	5.4	17	2,575	14.9	67	10.3	9	1,330	7.7

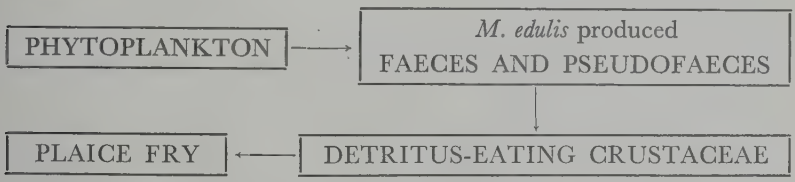
* Edwards *et al.* (1969).

** W': wet weight converted to cal.

*** Second hypothesis: metabolism is a function of food intake rate (Edwards *et al.* 1970); in the Flødevigen experiment being close to Q.

to the high phytoplankton production previously mentioned. The temperature condition was uncontrolled, but appeared to be within the survival limits of the organisms.

The main energy flow in the basin is supposed to have followed this simplified route:



The studies on metabolism carried out by Edwards *et al.* (1969, 1970) give an opportunity to backcalculate the food intake in the basin, based on the observed growth and information about the temperature conditions. Although rather sporadic observations on growth and temperature, such calculations have been carried out according to the two hypothesis of Edwards *et al.* (1970).

1. Metabolism = 2Q
2. Metabolism is a function of food intake rate (see Appendix).

The two sets of calculated values are given in Table 3.

The table shows that the gross growth efficiency, K, according to the first hypothesis, is 4—6% most of the time. The daily food intake is high compared with the body weight and decreased from about 80% ($I_1 \times 100/W'$) in the beginning of the experiment to 20% at the end. The accumulated food intake per fish fry for 105 days was about 15 kcal, giving a mean gross growth efficiency of 5.4% for the whole growth period. The fry population consumed food of about 3 600 g wet weight, being equivalent to 2 600 kcal.

The second hypothesis gives a metabolism practically equal to resting metabolism, Q. Consequently the food intake, I_2, was half of the above calculations. The gross growth efficiency was 8—11% most of the time (Table 3), and the food intake as a percentage of the body weight reached a value of 10% in late September although it was 20—40% most of the time. The accumulated food intake per fry was about 8 kcal, giving a mean gross growth efficiency of 10%. The total food consumption by the population was about 1 800 g wet weight, being equivalent to 1 300 kcal.

Edwards *et al.* (1969) observed a reduction in active metabolism with increasing temperatures above 10 °C. Further they observed that the active metabolism at 20 °C was nearly the same as the resting metabolism at that temperature. Due to this Edwards *et al.* (1969) suggest that 20 °C might be a possible upper limit for survival. The fish in the basin survived for a long period at this supposed critical temperature and had a high daily food consumption (Table 3). The critical temperature might therefore be higher than the suggested 20 °C, implying a laboratory artifact in their experiments. Further the resting metabolism might have been considerably lower than the active metabolism permitting the fry to hunt for food and digest it. The high resting metabolism might be due to laboratory stress as suggested by Edwards *et al.* (1969). After all, it seems reasonable to assume that the active metabolism, E, of the fry in the basin was equal to the observed Q, but in this case Q represent the active metabolism under the actual feeding and temperature regime.

The stomach contents on 28 September give support to this view as the mean calorific contents of the five investigated guts at 1200 hours was calculated to be 10 cal. Assuming a steady food intake for 16 hours and that the gut contents at 1200 hours represented the food eaten since 0800 hours, the plaice fry consumed 40 cal until 2000 hours. This is more in agreement with the calculated food intake of 67 cal according to the second hypothesis than to 127 cal according to the first hypothesis (Table 3). As the metabolism of E = Q seems to be a more reliable estimate in the basin experiment, this will be used in the following calculations.

According to both hypothesis, the density of food close to the bottom needed to be rather high. A newly metamorphosed plaice can effectively search 3 litres/day with a 16 hour feeding time (Blaxter and Staines 1971); therefore, at the start of the experiment the fish must have captured 10 cal/litre to obtain 30 cal (Table 3). The food density had to be even higher as some of the water was searched several times by several fry, and also there had to be prey animals surviving to ensure production in the future. Calculation of the calorific content per litre can be carried out according to Ware (1975):

$$I = \frac{v\gamma\varrho}{1 + \gamma v h \varrho}$$

A food intake of 3 cal/hour (I), a search volume of 0.2 litre/hour (γv) and consumption time of 0.04 hour/cal (h), using the value from Ivlev (1960) for bleak (*Alburnus alburnus*), gives a density, ϱ, of 17 cal/litre as an estimate for organisms living close to the bottom. Thijssen, Lever

and LEVER (1974), studying the feeding intensity of 0-group plaice, observed a food intake of 18 cal from 0500 hours to 0800 hours which gives 0.10 hour/cal. As those plaice were bigger than these in this experiment, it is more likely that the consumption speed in the basin was somewhat slower, and assuming a search time of 0.20 hour/cal, the density of food close to the bottom had to be 38 cal/litre. The actual minimum production rate of prey animals in the basin had to be 13 kcal per days as a mean value, being equivalent to about 10 g wet weight. With an assumed mean gross growth efficiency of 15% at the ambient temperature (GAUDY 1974), the consumption of detritus by the everte-brates was probably about 60 g wet weight per day.

With an assumed growth rate of 10% (CHANG and PARSONS 1975), the standing stock of prey organisms must have been at least 100 g wet weight, giving 2.9 cal/litre. This density seems to be rather low, but as the main prey organisms were semipelagic, being distributed close to the bottom, an assumed distribution within a 10 cm range over the bottom gives about 40 cal/litre as a close to the bottom value which is in agree-ment with the earlier calculations.

The discrepancy in growth and survival between this basin experiment and the tank experiments referred to, seem to originate from the character of the ecosystem into which the fry were introduced. The key to the applied system, which gave a comparatively high growth rate and survival of the plaice fry at high stocking density and at unfavourable temperature conditions, seems to be the harvesting of phytoplankton by *M. edulis*. The faeces gave a high food supply to the detritus-eating crustacea which in turn served as food for the plaice.

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APPENDIX

The resting metabolism expressed in cal/day is (Edwards *et al.* 1969, 1970):

$$Q = 0.214 \times 4.8 \times 24 \times W^{0.721}(1 + 0.1\ Q_{10}(t-10)) \text{ where}$$

W is gram wet weight derived from $W = 0.00805\ l^3$,

4.8 is the oxycalorific coefficient

Q_{10} is in the temperature range 10—15 °C 3.6 and
in the temperature range 15—20 °C 5.6

The calorific value of young plaice is in the range of 4.8—5.2 kcal/g dry weight. Applying a mean value of 5 kcal/g dry weight and a conversion factor of 5:1 for live to dry weight, 1 g wet weight becomes equivalent to 1 kcal.

The daily food intake, I, is:

$$I = \frac{G' + E}{\tau} \text{ modified from Ware (1975)}$$

where G′ is the growth expressed in cal/day and
E the metabolism in cal/day including standard metabolism and swimming cost.

$$\tau = p - s$$

where p is the assimilation factor and
s the specific dynamic effect of food (SDA) and loss of chemical energy in the urine. The suggested value of τ is $0.86 - 0.16 = 0.70$ (Ware 1975).

The first hypothesis of Edwards *et al.* (1970) suggest that $E = 2Q$. Therefore, according to the above suggested value 0.7 for food efficiency, the daily food intake will be:

$$I_1 = \frac{G' + 2Q}{0.7}$$

According to the second hypothesis of Edwards *et al.* (1970), metabolism is a function of the food intake rate. In Edwards *et al.* (1970) an average curve for food intake, I_2, is suggested and is indicated on their Fig. 9, page 169. In the present paper an equation for this curve has been calculated to be:

$$Y = 0.8\,X + 0.4 - \frac{4.4 - \sqrt{4.4^2 - 4\,X^2}}{2}$$

where $Y = \frac{I_2}{I_1}$ and

$$X = \frac{G'}{Q}$$

giving $$I_2 = I_1 \left(\frac{0.8\,G'}{Q} + 0.4 - \frac{4.4 - \sqrt{4.4^2 - 4\left(\frac{G'}{Q}\right)^2}}{2}\right)$$

The relationship between food intake and concentration of food is:

$$I = \frac{v\gamma\varrho}{1 + \gamma v h \varrho}$$ (Ware 1975)

where γv is the water volume effectively searched through by the fry,
ϱ is calories of food/litre and
h is the time required to capture and consume one calorie of food.

The calorific value of the food organisms was taken as 5.6 kcal/g dry weight (Comita and Schindler 1963) and 1 g wet weight became equivalent to 0.72 kcal (Ivlev 1960).

The specific daily growth rate (Shelbourne, Brett and Shirahata 1973) is:

$$SDG = \frac{(\ln W_1 - \ln W_0)100}{T_1 - T_0}$$

where T is time in days.

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INDIVIDUAL GROWTH RATE AND AGE AT FIRST SEXUAL MATURITY IN ATLANTIC SALMON

By

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ABSTRACT

Nævdal, G., Holm, M., Lerøy, R. and Møller, D. 1978. Individual growth rate and age at first sexual maturity in Atlantic salmon. *FiskDir.Skr.Ser.HavUnders.*, *16*: 519—529.

Growth rates and possible connection between growth rate and age at maturation were studied on individually tagged salmon originating from different river populations.

Great variations in growth rate and in age at first maturity were found among sib-groups of salmon originating from different populations (localities). Although much less pronounced, variations in these traits were also noted among groups within the localities.

When separating the individuals into groups according to age at first maturity, small variations were found within populations for smolt size, size after one summer and size after one year in the sea. The correlation between age at maturation and earlier growth rate thus seems to be rather small.

Significant correlations were found between size (length) at different times after the smolt stage both concerning the group means and the individual deviations from the means.

Mature female grilse stripped for eggs survived at about the same rate as immature fish during the spawning season while the survival rate of male grilse was considerably lower. Weight gain for immature fish during the same period was about two and a half time that of mature females and three times that of mature males.

INTRODUCTION

In two previous reports (Nævdal *et al.* 1975, 1976) tentative results from experiments with selective breeding of Atlantic salmon, *Salmo salar*, in Norway have been dealt with. The experiments started in autumn 1971 when fertilized eggs from several river populations and one fish

farm were collected. Since then, new material has been collected each year although gradually more emphasis has been laid upon selected parent fishes from the first two year classes.

The first year classes were used to study the variability in traits of economical importance for fish farming, especially growth rate and age at first sexual maturity. The influence of genetic factors on these traits were estimated from full sib and half sib correlations.

The fish of the first year class of these experiments were individually tagged which enables more detailed studies on correlation of growth rates at different ages and the possible connection between growth rate and age at sexual maturation. The aim of the present report is to analyse the data on the individually tagged fish in order to throw light on the topics mentioned above.

MATERIAL AND METHODS

The material used and the rearing methods are described in the previous reports (Nævdal *et al.* 1975, 1976).

The parent fish for the first year-class (1972) were collected from the following Norwegian rivers: Målselv, Lakselv, Lonevågselva, Lærdalselva, Rauma, Etneelva, Tengselva, Gaula (Sunnfjord), Opo, Eio and Vosso. Material from one Swedish (Skellefteälv) and two Canadian rivers (MacDonald River and Maria Pond) were also included as well as eggs of farmed salmon from one fish farm (Eros Laks, Bjordal). Eggs for two to ten (usually four) sib groups from each locality were collected, but some groups died or were drastically reduced during early rearing, mostly because of *vibrosis*.

Two years old, most of the fish reached smolt size in spring 1974. In some groups there were still some parr after two years. For practical reasons all fish were handled as smolt and transferred to sea water in spring 1974.

About 20 smolts, totally about 1000, of each surviving group were tagged with Carlin tags (Carlin 1955) in May 1974 and transferred to a fish farm, Svanøy Stiftelse, Svanøybukt, (Svanøy foundation) where they were kept in a 100 m^3 floating pen. The rest of the smolts were transferred to another fish farm, Risnefisk, Brekke, where they were kept in 50 m^3 floating pens for one year. Four to seven sib groups, marked with combinations of fin removal, were kept in each pen. In april 1975 maximum 100 fish of each sib group were tagged with numbered FT–4 «Lock on tags» (Floy Tag and Manufacturing Inc., Seattle) and transferred to Svanøy Stiftelse farm where they were kept in 500 m^3 floating pens. In

September the same year the Carlin tagged fish were transferred into the same pens as the Floy tagged fish.

Total lengths were measured each spring and autumn for fish of this year class, except that the Carlin tagged fish were measured one month earlier than the others in autumn 1974 and not measured at all in spring 1975. In 1976 the fish were measured in late June only. Individual weights were recorded for the tagged fish except for at the first measurement. Data on sex and of state of maturity were recorded when possible by external observation and at slaughtering in August 1976.

Due to fouling with mussels and sea weed, loss of the FT–4 tags was heavy, and the results therefore are based on considerably lower numbers within groups than planned. Tag loss by the Carlin method was insignificant, but about one third of the tagged fish were lost during the first summer. The results of the tagging experiments have been described in a separate report (Nævdal, Holm and Knutsson 1977).

Standard methods of calculating correlation and regression coefficients, means, standard deviations etc. were used (cf. Sokal and Rohlf 1969). The calculations of correlations of individual growth rate at different ages were made using deviation from the mean of all fish from the same locality measured in standard deviations. To reveal causes of variations, standard methods of analysis of variance were used (Bonnier and Tedin 1940).

RESULTS

VARIATIONS IN GROWTH RATE AND AGE AT FIRST MATURITY

Data on mean lengths and weights of the different sib groups were given in previous reports (Nævdal *et al.* 1975, 1976).

Variations in growth rate (measured as length or as weight) were great at all ages. Especially the variations between localities were pronounced, although some variations between sib groups within localities also were noted. The variation is illustrated in Fig. 1, which shows mean weights in June 1976 (25 months in the sea) for the groups pooled for river origin.

Estimates of heritability factors have been made (Nævdal *et al.* 1976), and usually high values were obtained. The use of the heritability concept is, however, somewhat dubious in this particular case since the high values mainly reflect variation between populations.

Incidences of maturing fish in the first (mainly small males resembling precocious parr), the second and the third sea year varied considerably. In Fig. 2 percentages of mature fish during the second (1975) and third (1976) sea year respectively, are presented. Fish mature in 1975 were

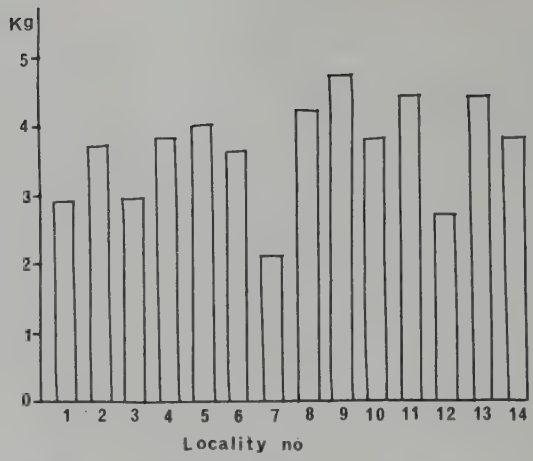

Fig. 1. Mean weights of salmon from different river localities after 25 months in the sea. Each locality represents from two to four sib groups.

regarded as mature in 1976 regardless of whether their gonads were ripening or not in 1976. Also for this trait the variations were most pronounced between localities, but variations were also noted between sib groups within localities (not shown in Fig. 2). Calculations of heritability factors gave high estimates, but a great part of the variation is assumed to be caused by additive gene effect, reflecting variation between populations.

INDIVIDUAL GROWTH RATE AT DIFFERENT AGES

In the previous reports (NÆVDAL *et al.* 1975, 1976) correlation analysis of mean length of the same sib groups at different ages was performed. Correlation coefficients were low between mean lengths at the presmolt stages, but fairly high between measurements from the smolt stage and onwards. Omitting the presmolt stages and supplying with data from June 1976 (25 months in the sea) the data matrix of Table 1 was obtained.

To analyse correlation between individual size at different age, the lengths of the individually tagged fish at the different measurements were compared. To eliminate the variation between populations (caused by genetic factors or by possible systematic environmental variation),

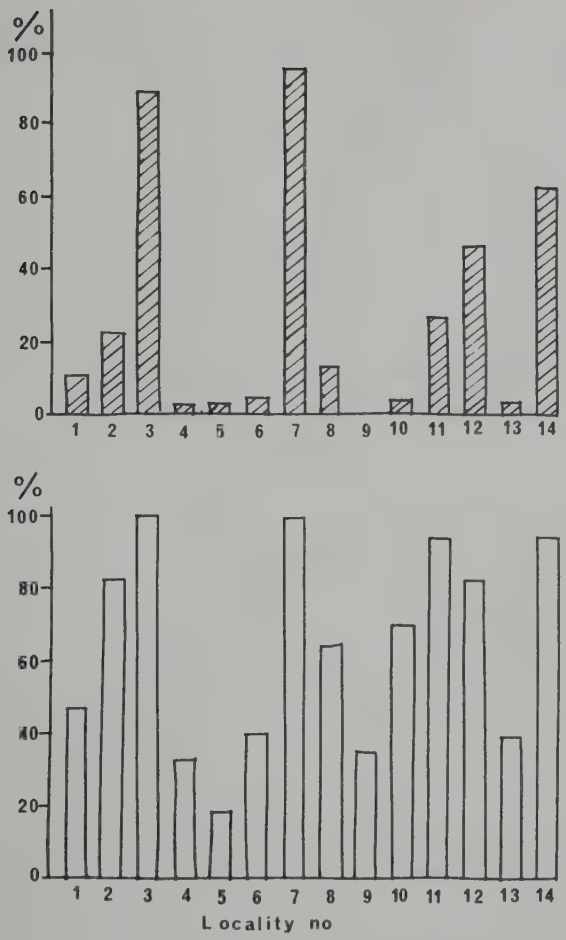

Fig. 2. Per cent mature fish the second (top) and third (below) sea year of salmon originating from different rivers reared under fish farming conditions.

individual deviations from the group means, measured in standard deviations, were used instead of absolute lengths. By using both Carlin tagged and Floy tagged fish, the correlation coefficients in Table 2 were found.

The correlation coefficients are in the same order of magnitude for individuals within populations as for means of sib groups. After the smolt

Table 1. Correlation coefficients (above diagonal) and coefficients or regression (below diagonal) of mean length of sib groups of salmon measured at five different ages.

Months in the sea	0	5	11	16	25
0	—	0.69	0.64	0.50	0.59
5	2.04	—	0.93	0.72	0.62
11	1.72	2.04	—	0.76	0.56
16	1.87	2.15	1.00	—	0.85
25	2.59	0.85	0.65	1.21	—

Table 2. Correlation coefficients of length (deviation from group means measured in standard deviations) of salmon at four different ages.

Months in the sea	0	4	16	25
0	—	0.69	0.53	0.37
4		—	0.71	0.63
11			0.84	0.67
16			—	0.87
25				—

stage, both individual growth rate and mean growth rate of the sib groups are rather highly correlated with size at later ages.

RELATIONSHIP OF AGE AT FIRST SEXUAL MATURITY WITH GROWTH RATE

The Carlin tagged smolt were seperated according to population, sex and fish maturing the second year in the sea, the third year in the sea or later. To see if there was any connection between smolt size (length) and some of the mentioned factors, an analysis of variance, Table 3, was performed.

At smolt stage, influence of sex seems to be insignificant. As expected the influence of populations is highly significant representing variation caused by genetic factors and possibly systematic environmental variations. Influence of age of maturation is possibly significant, and from the data it is seen that within some of the populations the fish maturing as grilse tend to be slightly bigger as smolt than the later maturing fishes.

In table 4, a corresponding analysis of lengths after one summer in the sea (for Carlin tagged fishes that means about 4 months) is shown. Also

Table 3. Analysis of variance of smolt size distributed on sex, population and age at first maturation.

Source of variation	d. f.	Mean squares	P
Between sex ...	1	0.80	> 0,2
Within sex	375		
Between river .	26	19.15	< 0,001
Within river ..	349		
Between age at first maturity ..	44	2.64	~ 0,05
Within age	305	1.83	

Table 4. Analysis of variance of length at one sea summer distributed on sex, population and age at first maturation.

Source of variation	d. f.	Mean squares	P
Between sex ...	1	1.23	> 0,2
Within sex	366		
Between locality	26	37.43	< 0,001
Within locality	340		
Between age at first maturation	45	9.55	~ 0,05
Within age	295	6.14	

here the influence of sex is insignificant, and influence of populations highly significant. Influence of age at first maturation is possibly significant, but it is impossible to see a general trend when comparing the mean lengths.

A corresponding analysis is shown in Table 5, but the data used are lengths after 11 months in the sea, i.e. half a year before maturation of the grilse. Only Floy tagged fish could be used. The conclusion will here

Table 5. Analysis of variance of length of salmon after one year in the sea.

Source of variation	d. f.	Mean squares	P
Between sex ...	1	10.4	> 0,2
Within sex	1143		
Between locality	24	593.4	< 0,001
Within locality	1119		
Between age at maturation	43	27.4	~ 0,05
Within age	1076	19.1	

be the same as in the former analysis; the length of the salmon after one year in the sea is not influenced by sex, greatly influenced by locality of origin and possibly influenced by age of which the fish are destined to mature.

Table 6. Analysis of variance of length of salmon after one year in sea.

Source of variation	d. f.	Mean squares	P
Between locality	12	1129.2	$< 0{,}001$
Within locality.	1133		
Between age at maturation	24	41.8	$> 0{,}2$
Within age	1108		
Between sex ...	27	32.6	$\sim 0{,}05$
Within sex	1076	19.2	

However, by eliminating first the influence of locality, then possible influence of age of maturation, the results in Table 6 were obtained.

Influence of locality is still strong, but influence of maturation age cannot be found by this method of analysis. However, influence of sex is probably significant when eliminating first the influence of locality. The reason for this is probably that influence of sex is more pronounced in some populations than in others. From the data it is evident that even at this stage the males are significantly smaller than the females within one of the localities. This might explain why the analysis of variance showed significant differences when testing influence of sex within localities, but not when testing it on the total material.

SURVIVAL AND GROWTH RATE OF MATURE SALMON

Survival and growth rate (weight gain) during the spawning season of fish maturing as grilse compared to immature fish are shown in Table 7. Because of a rather heavy tag loss during the actual period, survival of mature fish is given in per cent surviving compared to immature fish, assuming that tag loss was the same for mature and immature fishes. All females were stripped for eggs. The table shows that survival of females after spawning (stripping) is about the same as of immature fish while there is somewhat higher death rate of males. However, weight gain of females is less than the half compared to immature fishes, while it is still lower for males. The individual data also showed that there was great variation especially for the males, probably reflecting the observation that some mature fish start to eat soon after spawning while others start

Table 7. Survival and growth rate of immature and mature salmon (September 1975 to June 1976). The groups are pooled for each river. Survival of mature salmon in per cent of surviving immature and mean weight increase in kg.

Locality	Immature	Females		Males	
No.	mean weight	survival	mean weight	survival	mean weight
1	1.72	—	—	100	0.65
2	2.42	100	1.24	100	0.89
3	2.22	100	1.21	100	0.77
4	2.31	0	—	100	0.80
5	2.33	100	2.10	100	1.14
6	2.12	88	0.30	100	1.36
7	—	100	0.85	94	0.60
8	2.61	97	0.65	100	0.53
9	2.78	—	—	—	—
10	2.69	98	0.43	82	0.92
11	3.19	88	1.14	90	1.00
12	1.61	100	1.60	76	0.73
13	2.47	89	0.80	100	1.00
14	2.15	100	1.33	100	0.87
15	2.95	100	0.74	100	0.99

again later or not at all. Of the grilse 68.4 % were found to mature again the next spawning season. This figure was practically the same for both sexes.

DISCUSSION

The great variation in growth rate and age at first maturity among populations and sib groups seems to have a genetic base, although some of the variation may be caused by systematic environmental variation because the populations usually were kept in separate floating pens until the fish were individually tagged. Great variations, probably with a genetic base, have also been found in later year classes in the same experimental series (unpublished). It therefore seems clear that salmon used for fish farming purposes in Norway is of varying value concerning their ability of growth and especially concerning their age at first maturation. Selection of populations, probably also of individuals within populations, seems promising and is now under way.

The importance of late maturation in fish used for fish farming is clearly shown by the differences in weight gain by the salmon maturing as grilse and the salmon not maturing during their second year. Although the death rates for mature and immature fish were not so different as expected and as claimed by the fish farmer, the weight gain during the spawning season and until next summer was less than the half of mature fish compared to the immature ones. Surprisingly, both the weight gain and survival rate were higher for mature females than for males.

The growth differences between males and females were not very pronounced until maturation and could not be seen when looking at the total material. Within populations, however, such differences seemed to excist, and the populations probably are different concerning this trait. Especially in the groups from one of the localities the males were significantly smaller than the females half a year before maturation.

The analysis of variance, performed to investigate any possible connection between growth rate and age of maturation, gave no clear answers. There seemed to be some variation in growth rate which could be connected with the fish's maturation later on, e.g. the smolt size of the grilse seemed to be somewhat greater than the smolt size of larger salmon, and a similar tendency was found concerning size after one year in the sea, although not very pronounced.

Ritter (1975) reports that within groups of hatchery reared smolt, the larger smolts produce proportionally fewer grilse than did the smaller ones. In the present study it is not possible to find such a tendency within groups, on the contrary in the total material and within some populations there seems to be tendency to a somewhat higher mean for smolt size of the grilse than of the larger salmon. A similar tendency has been found for coho salmon by Hager and Noble (1976).

Correlations of growth rates were found to be in the same order of magnitude for sib group means as well as for individual deviations from population mean. The correlation coefficients were all significant, and even smolt size correlated well with the size of the fish at later ages. However, low correlation was found between presmolt growth rate and the growth rate in the sea (Nævdal *et al.* 1976).

The rather high correlations which were found, are of some importance for making selection for higher growth rate. High correlations imply that selection both of sib groups and of individuals within sib groups can be made earlier than at normal slaughtering age, thus reducing the cost of rearing of experimental fish. However, more data on this is needed, and it is also evident that the residual (error) variance is rather great implying that other factors than size at a given time may have considerable influence on the size at slaughtering.

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A FISHING EXPERIMENT WITH MULTIFILAMENT, MONOFILAMENT AND MONOTWINE GILL NETS IN LOFOTEN DURING THE SPAWNING SEASON OF ARCTO-NORWEGIAN COD IN 1974

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ABSTRACT

HYLEN, A. and JAKOBSEN,T. 1979. A fishing experiment with multifilament, monofilament, and monotwine gill nets in Lofoten during the spawning season of Arcto-Norwegian cod in 1974. *FiskDir. Skr. Ser. HavUnders.*, *16* : 531–550.

From 6 February to 30 March 1974 during the spawning migration of Arcto-Norwegian cod, a fishing experiment with gill nets made of continuous multifilament nylon, nylon monofilament and nylon monotwine was carried out in Lofoten.

The different types of nets were combined to make up one gill net setting consisting of 40 to 92 single nets, half of which were multifilament nylon nets and one quarter each monofilament and monotwine nets. The sequence of the single nets was varied during the experiment.

The result for the total experiment was that the monofilament nets caught 26% (in numbers) more cod than the multifilament nylon nets and 38% more than the monotwine nets. For saithe the monotwine nets were apparently the most and the multifilament nylon nets the least efficient.

The average length of the captured fish was slightly higher for the multifilament nylon than for the monofilament nets whereas the fish caught by the monotwine nets were somewhat smaller.

Taking the length frequency of cod caught by purse seine in the same area during the experiment as representative for the cod available to the gill nets, a log-normal distribution selection curve was fitted for each of the three types of gill nets.

The mesh size used in the experiment (186 mm) was clearly too small to obtain maximum catches of the available cod. Assuming proportionality between mesh size and mean selection length gave optimum mesh sizes of 224 mm for nylon, 222 mm for monofilament and 234 mm for monotwine. The ratios between the theoretical maximum catches thus obtained were: Monofilament: Nylon = 1.46; Monotwine: Nylon = 1.48; Monotwine: Monofilament = 1.02.

Assuming that all length groups are equally numerous among the cod available to the nets, ratios between the catch efficiency of the three nets, which should represent a more general situation, were calculated, giving: Monofilament: Nylon = 1.23; Monotwine: Nylon = 1.15; Monofilament: Monotwine = 1.07. However, the accuracy and the general validity of these ratios are dependent on several factors of which the environmental conditions may be the most decisive.

INTRODUCTION

For nearly twenty years continuous multifilament nylon has been the common material in gill nets used in the Norwegian cod and saithe fisheries. During the last few years some fishermen have changed over to monofilament gill nets and the interest taken in these nets seems to be increasing. In Europe, monofilament gill nets have up till now been used mainly in freshwater fisheries and in saltwater fisheries for salmon. In some other areas, however, particularly in the Far East, they are widely used in marine fisheries.

A few experiments designed to compare the fishing efficiency of monofilament gill nets with gill nets made of other types of synthetic fibres have been carried out (e.g. MOLIN 1959, STEINBERG 1964, MAY 1970). In most cases the results imply that the monofilament gill nets are superior to the others, and the authors generally ascribe this to lower visibility of monofilament nets in water. Results of experimental fishing for gadoids have, however, to the best of our knowledge so far not been published.

Under the supervision of the Institute of Marine Research in Bergen, experimental fishing in order to compare the fishing efficiency of monofilament and multifilament nylon gill nets was carried out in Lofoten in 1974 during the spawning season of the Arcto-Norwegian cod. Also monotwine gill nets, which recently have been the object of some interest, were included in the experiment.

MATERIALS AND METHODS

The materials used for the gill nets were: Continuous multifilament nylon 210/12, nylon monofilament 14 (0.65 mm), and nylon monotwine 5/3. The basic characteristics of these materials regarding this experiment are as follows:

Monofilament is made of a single thin and nearly transparent thread which presumably has low visibility in water.

Continuous multifilament is made by a number of fibres spun into a yarn. The visibility in water is obviously higher than for the monofilament.

Monofilament is stiffer and more elastic than multifilament yarn. In case of strong water movement, the stiffness may help to prevent the meshes from closing.

The monotwine consists of a number of monofilament wires, in this case three, which are twisted into a twine. It is thicker than the corresponding monofilament, and the visibility in water is accordingly higher, but probably less than for the multifilament. The twisting reduces the elasticity.

For the sake of simplicity, continuous multifilament nylon is hereafter referred to as nylon only, nylon monofilament as monofilament, and nylon monotwine as monotwine.

The net units were 300 meshes long and 50 meshes deep. The dimension of the nets was the same for all three materials, corresponding to a mesh size of 186 mm. In practice, the mesh size of the different materials was in average (before and after use): Nylon: 188/192 mm. Monofilament: 185/182 mm. Monotwine: 184/180 mm. For all three types, however, considerable deviations from the mean mesh size were frequently observed.

One half of the units in the gill net setting were made of nylon and one quarter each of monofilament and monotwine.

It was suspected that the catch in addition to fishing efficiency of the different net types, might be influenced by the number of nets of the same type in sequence and also by the position of the nets in the setting and relative to the other types of nets (von BRANDT 1955). To ensure that the experiment would give the best possible information about the influence of these factors, the sequence of units of different materials in the setting was chosen by the following procedure: The units of each material were assembled into groups of different numbers. Each group was joined to the corresponding groups of the other two materials to make up «triplets» of n monofilament units, n monotwine units, and $2n$ nylon units. The sequence of materials in the «triplets» was the same throughout the gill net setting in order to make sure that groups of the same material were not joined. The sequence of the «triplets» was decided at random and was changed three times during the experiment. The number of units used in the settings varied from 40 to 92. Table 1 shows the sequence used at the different stations during the experiment. In addition, as often as practically permissable, the position of the setting relative to the main direction of the migration of the cod was changed so that one end alternatively would be nearest to or farthest away from shore.

Two fishing boats were hired for the experiment: «Djupaskjær» (64 ft.) 6–28 February and «Skarsjø» (62 ft.) 4–30 March.

The gill net settings made during the experiment are listed in Table 2 and charted on Fig. 1. The nets were always set by daylight and hauled in the morning before noon. In most cases they were left for one night, on five occasions for two nights, and twice for three nights. On eight occasions the gill nets were set as floating nets.

A record was kept of the fish caught in each net unit. All fish were measured.

Table 1. Sequence of nets used at different stations during the fishing experiment in Lofoten in 1974.
N = Continuous Multifilament Nylon, MF = Nylon Monofilament, MT = Nylon Monotwine.

Station No.	Sequence of nets	Total No.
1–2	6N – 3MF – 3MT – 10N – 5MF – 5MT – 4N – 2MF – 2MT	40
3–5	6N – 3MF – 3MT – 10N – 5MF – 5MT – 4N – 2MF – 2MT – 14N – 7MF – 7MT	68
6–8	6N – 3MF – 3MT – 10N – 5MF – 5MT – 4N – 2MF – 2MT – 14N – 7MF – 7MT – 1N	69
9–14	4N – 2MF – 2MT – 6N – 3MF – 3MT – 12N – 6MF – 6MT – 10N – 5MF – 5MT – 14N – 7MF – 7MT	92
15–23	6MF – 6MT – 12N – 3MF – 3MT – 6N – 7MF – 7MT – 14N – 5MF – 5MT – 10N – 2MF – 2MT – 4N	92
24–36	3MF – 3MT – 6N – 2MF – 2MT – 4N – 7MF – 7MT – 14N – 5MF – 5MT – 10N – 6MF – 6MT – 12N	92

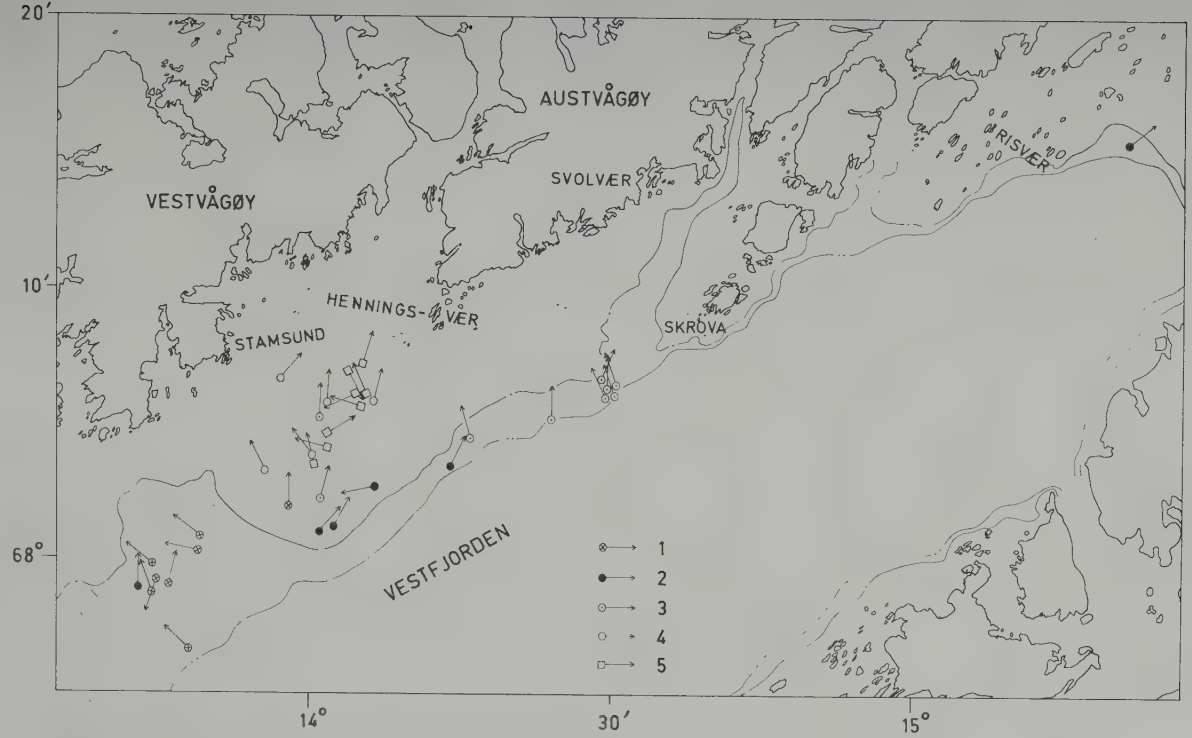

Fig. 1. Gill net settings during the comparative fishing experiment in Lofoten in 1974. 1) «Djupaskjær» 6—16 February, 2) «Djupaskjær» 18—28 February, 3) «Skarsjø» 4—15 March, 4) «Skarsjø» 18—27 March, 5) «Skarsjø» 15—30 March (Floating nets).

Table 2. Gill net settings and catches during the comparative fishing experiment in Lofoten in 1974. N = Continuous Multifilament Nylon, MF = Monofilament Nylon, MT = Monotwine Nylon, F = Floating net.

Station No	Fishing Vessel	Date	Position N	Position E	Hours Fishing	Fishing Depth (Fath.)	No. of nets N	No. of nets MF	No. of nets MT	Catch of cod Total No.	Catch of cod No. per net N	Catch of cod No. per net MF	Catch of cod No. per net MT	Catch of saithe Total No.	Catch of saithe No. per net N	Catch of saithe No. per net MF	Catch of saithe No. per net MT
1	«Djupaskjær»	6– 7/2	68°03'	13°58'	20	60 – 88	20	10	10	13	0.10	0.40	0.70	2	—	—	0.20
2	»	7– 8/2	67°57'	13°47'	20	75 – 90	»	»	»	5	0.20	—	0.10	3	0.10	—	0.10
3	»	8– 9/2	67°59'	13°44'	21	60 – 72	34	17	17	31	0.29	1.06	0.18	9	0.03	0.18	0.29
4	»	9–11/2	68°00'	13°43'	44	56 – 64	»	»	»	47	0.74	0.88	0.41	25	0.29	0.53	0.35
5	»	11–13/2	68°01'	13°48'	44	52 – 70	»	»	»	33	0.50	0.71	0.24	74	0.68	1.35	1.65
6	»	13–14/2	68°00'	13°47'	21	58 – 70	35	»	»	29	0.40	0.41	0.47	71	0.63	1.06	1.82
7	»	14–15/2	67°59'	13°44'	21	54 – 70	»	»	»	14	0.20	0.29	0.12	36	0.37	0.88	0.47
8	»	15–16/2	68°00'	13°47'	20	55 – 68	»	»	»	65	1.03	1.24	0.53	19	0.12	0.47	0.41
9	»	18–19/2	68°00'	13°43'	17	55 – 65	46	23	23	84	1.20	0.61	0.65	13	0.02	0.13	0.39
10	»	19–20/2	68°03'	14°05'	18	47 – 50	»	»	»	45	0.52	0.43	0.48	8	0.09	0.13	0.04
11	»	20–21/2	68°02'	14°03'	20	45 – 60	»	»	»	67	0.76	0.91	0.48	8	0.04	0.13	0.13
12	»	21–23/2	68°02'	14°02'	44	62 – 68	»	»	»	170	1.33	3.26	1.48	12	0.02	0.13	0.35
13	»	23–26/2	68°04'	14°15'	67	56 – 67	»	»	»	55	0.63	0.57	0.57	10	—	0.13	0.30
14	»	27–28/2	68°16'	15°23'	20	54 – 70	»	»	»	98	0.93	1.48	0.91	1	—	—	0.04
15	«Skarsjø»	4– 5/3	68°07'	14°30'	16	52 – 64	»	»	»	163	1.83	1.83	1.61	21	0.13	0.30	0.35
16	»	5– 6/3	68°07'	14°29'	16	52 – 62	»	»	»	67	0.67	0.87	0.70	16	—	0.22	0.48
17	»	6– 7/3	68°06'	14°24'	13	45 – 80	»	»	»	61	0.72	0.91	0.30	9	0.02	0.17	0.17
18	»	7– 8/3	68°07'	14°30'	14	70 – 75	»	»	»	22	0.22	0.17	0.35	23	0.20	0.09	0.52
19	»	8–11/3	68°07'	14°30'	69	62 – 65	»	»	»	69	0.91	0.78	0.39	9	0.07	0.09	0.17
20	»	11–12/3	68°06'	14°01'	12	60	»	»	»	172	1.48	2.30	2.22	1	—	—	0.04
21	»	12–13/3	68°03'	14°02'	13	45 – 50	»	»	»	291	2.87	3.91	3.00	4	0.04	0.04	0.04
22	»	13–14/3	68°05'	14°16'	19	40 – 60	»	»	»	96	0.89	1.04	1.35	2	0.02	—	0.04
23	»	14–15/3	68°07'	14°30'	15	50 – 64	»	»	»	34	0.41	0.48	0.17	91	0.52	0.74	2.17
										94	1.09	0.87	1.04	—	—	—	—

26	»	18–19/3	68°04'	14°00'	15	44 – 50	»	»	»	50	0.57	0.48	0.57	—	—	—	—
27	»	19–20/3	68°04'	14°00'	13	35 (F)	»	»	»	110	1.35	0.87	1.22	—	—	—	—
28	»	20–21/3	68°06'	14°02'	13	50	»	»	»	91	0.96	1.04	1.00	—	—	—	—
29	»	21–22/3	68°04'	14°00'	12	35 (F)	»	»	»	82	0.80	0.96	1.00	—	—	—	—
30	»	22–23/3	68°04'	13°55'	17	40 – 45	»	»	»	75	0.78	0.39	1.30	—	—	—	—
31	»	23–25/3	68°06'	14°07'	42	45 – 60	»	»	»	410	3.83	6.43	3.74	—	—	—	—
32	»	25–26/3	68°08'	14°06'	14	35 (F)	»	»	»	325	3.52	4.52	2.57	—	—	—	—
33	»	26–27/3	68°07'	13°58'	13	40 – 42	»	»	»	152	1.78	2.13	0.91	—	—	—	—
34	»	27–28/3	68°06'	14°03'	11	35 (F)	»	»	»	127	1.48	1.48	1.09	—	—	—	—
35	»	28–29/3	68°03'	14°05'	11	35 (F)	»	»	»	78	0.89	0.83	0.78	—	—	—	—
36	»	29–30/3	68°06'	14°04'	12	35 (F)	»	»	»	39	0.35	0.52	0.48	—	—	—	—

RESULTS

The total catch during the experiment was 3 487 cod, 486 saithe, 27 redfish, 8 anglers, 6 ling, 3 tusk, 2 haddock, 2 blue ling, 1 lumpsucker, 1 dogfish, and 1 ray. Thus, only cod and saithe were caught in quantities which might be sufficient to give significant information about differences in catch efficiency of the three types of nets used. Saithe smaller than 50 cm have been left out because the schooling behaviour of the small saithe resulted in a distribution of the catches which obviously could not be ascribed to differences in catch efficiency alone. The discussion is hence based on the catches of 3 487 cod and 467 saithe.

Total catch in numbers and catch per net unit of cod and saithe are given in Table 2 for each type of net and each setting. There was a large variation in total catch per setting. However, the distribution of the catches on the three types of nets was more consistent and in Table 3 the ratios between the catches from each type of net are given for each of the different net sequences used during the experiment (Table 1) and for the whole experiment. The ratios for saithe were much less consistent than for cod. This can probably be ascribed chiefly to the much higher number of cod caught.

The monofilament nets caught the highest number of cod per net, 26% more than the nylon nets and 38% more than the monotwine nets. The nylon nets caught 10% more cod than the monotwine nets.

The ratios for saithe show that there were large differences in the catch between the three types of nets. The monotwine nets caught the highest number of saithe per net, 50% more than the monofilament nets which in turn caught more than twice the number caught by the nylon nets. Accor-

Table 3. Ratios between the catch in numbers by nets of different material during the experiment in Lofoten in 1974. N = Continuous Multifilament Nylon, MF = Monofilament Nylon, MT = Monotwine Nylon.

	Station No.					TOTAL
	1 – 8	9 – 14	15 – 23	26, 28, 30, 31, 33	24, 25, 27, 29, 32, 34 – 36 (Floating net)	
Cod:						
MF/N	1.43	1.36	1.23	1.33	1.14	1.26
N/MT	1.35	1.17	0.99	1.05	1.17	1.10
MF/MT	1.97	1.59	1.22	1.40	1.33	1.38
Saithe:						
MT/N	2.40	7.00	4.89			3.46
MF/N	2.07	3.67	2.56			2.31
MT MF	1.16	1.91	1.91			1.50

dingly, the monotwine nets caught nearly three and a half time the number of saithe caught by the nylon nets.

The mean length of the captured fish was different for the three types of nets. For cod the mean length was 94.29 cm for nylon, 93,23 cm for monofilament and 89.75 cm for monotwine. The corresponding figures for saithe were 86.39 cm, 86.09 cm and 84.78 cm. This means that the ratios between the catches from the different types of nets change when the catch is converted from numbers to weight. Thus, the catch of cod by weight from the monofilament nets was 20% higher per net than from the nylon nets and 57% higher than from the monotwine nets. Accordingly, the nylon nets caught 30% more cod by weight than the monotwine nets. Also for saithe the conversion to weight favours the monofilament and nylon nets, but the catch from the monotwine nets was still considerably higher.

In the period 5–28 March, as part of routine investigations, cod was caught in Lofoten by purse seine. This fishing took place in the same area and during the same period «Skarsjø» carried out the gill net experiment. During this period the length frequency of the cod did not vary much in either the gill net or the purse seine catches which on an average were taken at approximately the same depth (88 m and 81 m respectively). The mesh of the purse seine was small enough to prevent selection of the available cod.

DISCUSSION

There are several approaches to the problem of assessing the selectivity of gill nets. The simplest or direct method requires that the size frequency distribution of the fish vulnerable to the nets is known or reliably estimated (Regier and Robson 1966). Thus, for a given net

$$S_l = \frac{n_l}{N_l}$$

where N_l is the absolute or relative number of fish of length stratum l vulnerable to the net and n_l is the number of fish of length stratum l caught by the net. If the selection index S_l is plotted for each l, a smooth curve can be drawn or a suitable mathematical function can be fitted to the points.

According to Rollefsen (1953) there is good reason to believe that purse seine catches of cod in Lofoten give a nearly unbiased length composition of the fish present. This idea was persued by Holt (1963) who used Rollefsen's (1953) data to find the selection curve for the gill nets used in Lofoten the same year. The data produced a nearly symmetrical distribution of selection indexes and Holt (1963) chose to fit a normal distribution curve to the set of points.

BARANOV (1914) assumed that the selection curves for gill net could be adequately described by the normal probability distribution. Also GARROD (1961) stated that if the growth of the fish is isometric, then the selection for length by gill nets of a given mesh size may be expected to have a normal distribution.

In some gill net fisheries, as observed by OLSEN and TJEMSLAND (1963) and JENSEN (1977), significant numbers of fish outside the main size range of the selection curves were caught by other ways of attachment than the usual with head first. Observations on brown trout by JENSEN (1977) indicated further that fish larger than those caught head first in a single mesh are more frequently caught than those that are smaller. This could be expected to give a positive skew of the curves describing gill net selection.

A pronounced positive skew in a gill net selection curve was found for brown trout by JENSEN (1977). Less pronounced positive skews have been observed, e.g. for herring by OLSEN (1959) and for lake whitefish by REGIER and ROBSON (1966) and the observations on gill net selectivity indicate a considerable variation in selectivity for different species of fish. The selection curve may deviate significantly from one that can be adequately described by a reasonably simple mathematical function (OLSEN and TJEMSLAND 1963). Wiht sufficent data it will be possible to fit a selection curve by eye, a method described by GULLAND and HARDING (1961) and used by JENSEN (1977). However, if a mathematical expression for a selection curve with a reasonably good fit to the observed selection indexes can be found, this may facilitate further discussions on properties of gill net selectivity.

According to HOLT (1963), one might expect that the chance of a fish escaping the nets depends not on the absolute amount, but on the proportion, by which its size differs from that size for which the net is most efficient. If the growth of the fish is isometric, and two lengths l_A and l_B are related by the equation

$$(1) \quad \frac{m}{l_A} = \frac{l_B}{m}$$

where m is the mean selection length of the gill net, the selection index for fish of length l_A should be equal to the selection index for fish of length l_B. Introducing logarithms in *(1)* and squaring give

$$(lnm - lnl_A)^2 = (lnl_B - lnm)^2$$

or

$$(2) \quad (lnl_A - lnm)^2 = (lnl_B - lnm)^2$$

A log-normal distribution curve is defined by the formula

$$(3) \quad f(l) = \frac{1}{s\sqrt{2\pi}} e^{-\frac{(lnl-lnm)^2}{2s^2}}$$

where l is the length, s the standard deviation of lnl and m the mean selection length corresponding to $\overline{lnl}$. Applying (2) to (3) gives $f(l_A) = f(l_B)$, and a selection curve with a log-normal distribution is therefore in accordance with HOLT's (1963) suggestion.

OLSEN (1959), MCCOMBIE and FRY (1960), and GULLAND and HARDING (1961) assumed that the mean selection length of a gill net is proportional to the mesh size. Thus, the mean selection lengths m_A and m_B for mesh size A and B respectively are related by the equation

$$(4) \quad m_B = cm_A$$

where $c = \frac{B}{A}$. HOLT (1963) suggested that the chance of a fish escaping the net is dependent on the proportion between the size of the fish and the mesh size. BARANOV (1914) assumed that the catch effeciency relating to the mean selection length is constant and accordingly independent of the mesh size. The selection indexes for a fish of length l_A and l_B will then be the same, if

$$(5) \quad \frac{l_A}{m_A} = \frac{l_B}{m_B}$$

Combining (4) and (5) gives

$$(6) \quad l_B = cl_A$$

and subtracting (4) from (6) gives

$$(l_B - m_B) = c(l_A - m_A)$$

i.e. the same proportionality excists between the length intervals $(l_B - m_B)$ and $(l_A - m_A)$ as between the mean selection lengths. The extension of the selection curve along the length axis is therefore proportional to the mean selection length and consequently to the mesh size.

For the log-normal distribution, keeping s constant, the selection indexes for l_A and l_B will be the same if $(lnl_A - lnm_A) = (lnl_B - lnm_B)$,

$$i.e. \quad \frac{l_A}{m_A} = \frac{l_B}{m_B} \; (5)$$

Consequently for a log-normal distribution curve the desired proportionality is obtained if the standard deviation is kept constant as the mean selection length varies, whereas for a normal distribution the standard deviation must be changed in proportion to the mean selection length to obtain corresponding results.

In the calculation of the selection indexes, the length frequency distribution of cod in purse seine catches from 1974 was used in basically the same way as HOLT (1963) used the data of ROLLEFSEN (1953). However, the cod caught with gill nets by «Djupaskjær» were on the average 2.38 cm longer

than those caught by «Skarsjø». This is in accordance with previous experience that the cod in Lofoten usually is bigger during the first part of the spawning season. Therefore, when selection indexes were calculated, the purse seine data were combined only with the data from the «Skarsjø» gill net catches which were taken contemporarily.

On Fig. 2 it can be seen that there is a tendency for the selection indexes to stop decreasing at a certain level on each side of the selection range, especially for the bigger length groups. The level is apparently about the same for the three types of nets. It was assumed that the selection indexes for the length groups nearest to the mean selection length represent fish caught with the head first, although these values probably also to some extent are influenced by fish caught in other ways. The selection curves were accordingly chosen in order to give the best fit for the medium selection indexes, and the resulting curves should approximate the selective properties of the gill nets for fish caught with the head first in a single mesh, ignoring other ways of being caught.

Excluding the extreme values, tests show no clear evidence of skewness, but although the log-normal distribution has a slight positive skew, the fit to the selection indexes is good for all three types of nets (Fig. 2). As has been shown, the log-normal distribution is consistent with certain aspects of the theory of gill net selectivity, and the remainder of the discussion has been based on the assumption that gill net selectivity for cod may be adequately described by the log-normal distribution.

When fitting a log-normal distribution, lnm and the standard deviation can be calculated from the selection indexes based on the actual catches. When

$$lnl = lnm,$$

then

$$f(l) = \frac{1}{s\sqrt{2\pi}}$$

and this defines the maximum of the curve. To make it fit the selection indexes, the vertical extention of the curve must be adjusted according to the sum of the selection indexes. Thus, fitting a normal distribution would have required a multiplication of the formula by 5 to adjust for the use of selection indexes for 5 cm length groups when the unit is cm. In the log-normal distribution, the transformation to logarithms means that a length interval of 5 cm no longer represents a constant unit, because

$$[lnl - ln(l - 5)] > [ln\,(l + 5) - lnl].$$

The selection indexes must therefore be weighted by the size of the interval they represent. The maximum for the log-normal distribution is accordingly defined as

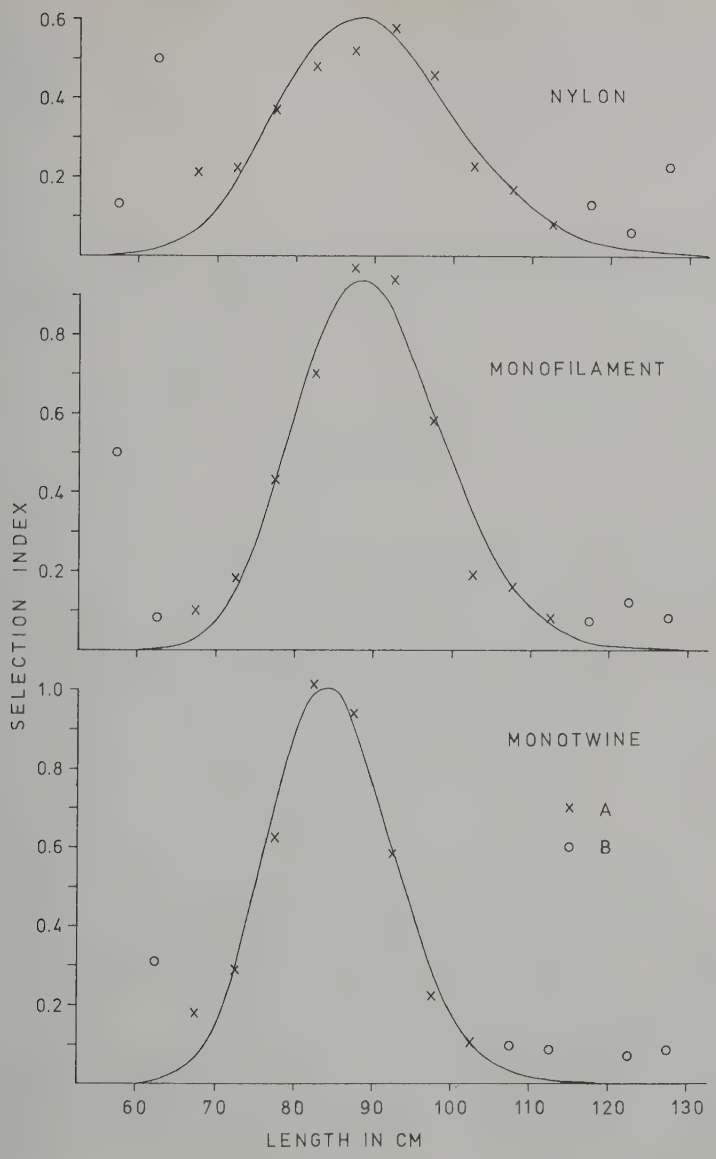

Fig. 2. Selection indexes and fitted normal and log-normal distribution selection curves for nylon, monofilament and monotwine gill nets based on fishing experiments in Lofoten 4—30 March 1974. A) Selection indexes included in the curve fitting. B) Selection indexes not included in the curve fitting.

$$f_{max} = \frac{\Sigma S_l \left[ln\,(l + 2.5) - ln\,(l - 2.5)\right]}{s\sqrt{2\pi}}$$

For each 5 cm interval l is defined as the middle length, i.e.

$$l = l_i + 2.5$$

where l_i is the lower limit of the interval.

The selection curves for the three types of nets are clearly different (Fig. 3). The parameters of the curves given in Table 4 show that the mean selection length is slightly (0.8 cm) higher for monofilament than for nylon whereas it is considerably higher (4.4 cm) than for monotwine. The peak efficiency (selection index for the mean selection length) is approximately the same for monofilament and monotwine. For nylon it is only about 60% of these values. However, the selection curve for nylon covers most length groups (has the largest standard deviation) whereas monotwine clearly covers least.

It is evident from Fig. 3 that the mesh used in the gill nets during the experiments was much too small to give maximum obtainable catches of the available cod. Taking the length frequency distribution of the purse seine catches as representative of the available cod, theoretical gill net catches obtained by varying the mesh size were calculated. The resulting theoretical maximum catches (by weight) were for nylon and monofilament respectively 1.9 and 2.2 times higher than the actual catches made by «Skarsjø». For monotwine the catches would have increased by a factor of 3.9. However, in practice the increase in catches would be expected to be slightly higher because there would have been additional fish caught in irregular ways, especially on the lower side of the selection range, which are not accounted for by the fitted selection curves. The optimum mesh sizes, neglecting the observed deviations from the official figure of 186 mm in the nets used during the experiment, were: Nylon: 224 mm, Monofilament: 222 mm and Monotwine: 234 mm. The theoretical maximum catches of monotwine and monofilament were not significantly different (MT: MF = 1.02) and both were considerably higher than the catches by nylon (MT: N = 1.48, MF: N = 1.46).

With the length range of the available cod in Lofoten in 1974, there was obviously a lot to be gained in catches by increasing the mesh size of the gill nets. However, the length distribution of the cod in 1974 was extreme, and the mesh size used will in an average year not by far deviate that much from the optimum.

The observed differences in catch efficiency between the three types of nets are valid only when the circumstances are very similar to those of the experiment. Probably the most obvious deviation from a general situation

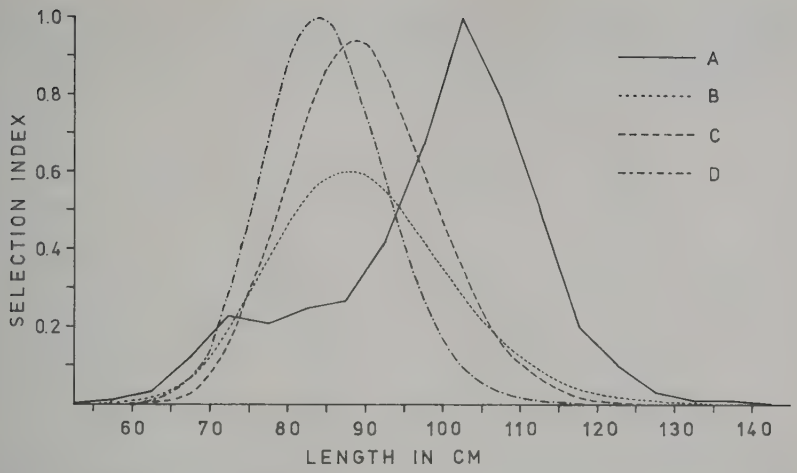

Fig. 3. Length frequency distribution (per cent) of cod caught with purse seine in Lofoten 5—28 March 1974 (A) and fitted log-normal distribution selection curves for B) nylon, C) monofilament and D) monotwine gill nets based on fishing experiments in Lofoten 5—30 March 1974.

Table 4. Parameters of log-normal distribution curves fitted to the calculated selection indexes for the three types of gill nets.

Type of net	Mean selection length (cm) [1]	Standard deviation	Maximum of curve
Nylon	87 612	0.12794	0.5993
Monofilament	88 394	0.10475	0.9395
Monotwine	83 950	0.09392	1.0000

[1]) This is the 1 corresponding to $\overline{lnl}$.

was the peaked length frequency distribution of the cod available to the nets which favoured the relative catch efficiency of nets with a narrow selection curve. However, a theoretical generalization of the relative catch efficiency of the nets can be made by assuming that all length groups are equally represented in numbers among the cod available to the nets. When the length intervals representing one length group are made infinitesimally small, the theoretical catch in numbers of fish by a gill net with a log-normal selection curve will be proportional to

$$\int_0^\infty h e^{-\frac{(lnl - lnm)^2}{2s^2}} dl$$

where h is the maximum, m the mean selection length and s the standard deviation of the selection curve. The intergral can be solved by substituting u for lnl which gives an integral of the form

$$C_1 \int_{-\infty}^{\infty} e^{-\frac{1}{2s^2}u^2} e^{B_1 u}\, du$$

which can be transformed into

$$C_2 \int_{-\infty}^{\infty} e^{-\frac{(u-B_2)^2}{2s^2}}\, du.$$

This allows the use of the equation

$$\frac{1}{s\sqrt{2\pi}} \int_{-\infty}^{x} e^{-\frac{(t-m)^2}{2s^2}}\, dt = \frac{1}{2}\left[1 + \operatorname{erf}\left(\frac{x-m}{s\sqrt{2}}\right)\right]$$

Further, applying the definition

$$\operatorname{erf} z = \frac{2}{\sqrt{\pi}} \int_0^z e^{-t^2} dt \text{ (error function)}$$

and the equation

$$\int_0^{\infty} e^{-t^2}\, dt = \frac{\sqrt{\pi}}{2}$$

the final result is

$$\int_0^{\infty} he^{-\frac{(lnl-lnm)^2}{2s^2}}\, dl = h\sqrt{2\pi}s\, e^{-\frac{2lnm + s^2}{2}}$$

The relative catch efficiency (CE) of two nets A and B with mean selection lengths m_A and m_B, standard deliations s_A and s_B and maxima of selection curves h_A and h_B respectively, will be

$$\frac{CE_A}{CE_B} = \frac{s_A\, h_A}{s_B\, h_B}\, e^{\frac{1}{2}(s_A^2 - s_B^2) + \ln \frac{m_A}{m_B}}$$

For $m_A = m_B$ the eqution is reduced to

$$(7)\quad \frac{CE_A}{CE_B} = \frac{s_A\, h_A}{s_B\, h_B}\, e^{\frac{1}{2}(s_A^2 - s_B^2)}$$

Using (7) and the parameters of the selection curves given in Table 4, the following ratios in catch efficiency by number were found: $MF : N = 1.277$, $MT : N = 1.216$ *and* $MF : MT = 1.050$. This indicates for a general situation in gill net fisheries for cod that the catch efficiency in number of fish for monofilament is 28 % higher than for nylon and 5 % higher than for monotwine, and the catch efficiency of monotwine is 22 % higher than for nylon.

The theoretical catch by weight can be found by introducing a length-weigth relationship defined by the formula

$W_l = k_1 \cdot l^{k_2}$

The theoretical catch by weight will then be proportional to

$$\int_0^\infty h e^{-\frac{(lnl - lnm)^2}{2s^2}}\, k_1\, l^{k_2}\, dl.$$

The integral can be solved by the same procedure as for the catch in number. The final result is

$$\int_0^\infty h e^{-\frac{(lnl - lnm)^2}{2s^2}}\, k_1 2^{k_2}\, dl = h\, k_1 \sqrt{2\pi}\, s\, e^{(k_2 + 1)lnm + (\frac{1}{2}k_2^2 + k_2 + 1)\, s^2}$$

The relative catch efficiency *(CE)* of two nets, A and B, with mean selection lengths m_A and m_B, standard deviations s_A and s_B and maxima of selection curves h_A and h_B respectively, will be

$$\frac{CE_A}{CE_B} = \frac{s_A\, h_A}{s_B\, h_B}\, e^{(\frac{1}{2}k_2^2 + k_2 + 1)\,(s_A^2 - s_B^2) + (k_2 + 1)\ln \frac{m_A}{m_B}}$$

For $m_A = m_B$ the equation is reduced to

$$(8)\quad \frac{CE_A}{CE_B} = \frac{s_A\, h_A}{s_B\, h_B}\, e^{(\frac{1}{2}k_2^2 + k_2 + 1)\,(s_A^2 - s_B^2)}$$

The ratio is strongly dependent on the values of s and h which define the selective properties of the nets, but it is independent on m, the mean selection length. The ratio is dependent also on the value of k_2 in the formula $W_l = k_1\, l^{k_2}$. The effect of increasing k_2, is to change the ratio in favour of the net with the highest standard deviation, i.e. the widest selection curve.

An implication of the theoretical basis for arriving at the ratio equation (8) is that the girth is proportional to the length. Assuming that the growth is isometric, the volume and accordingly the weight, will be proportional to the cube of the length, providing that the specific weight is constant. To avoid inconsistency, the length-weight relationship used in the ratio equation should therefore be $W_l = k_1\, l^3$, i.e. $k_2 = 3$. In practice, length-weight data indicate that the true value may deviate somewhat from 3. However, for the most important roundfish species, the deviation is not large, and values within the usual range of k_2 calculated for cod on other occasions would have produced errors in the calculated catch efficiency ratios of less than ± 1% if substituted in (8).

Using (8) with $k_2 = 3$ and the characteristics of the selection curves given in Table 4, the following ratios of catch efficiency were found: MF: N = 1.226, MT: N = 1.149 and and MF: MT = 1.067. This indicates for a general situation in gill net fisheries for cod that the catch efficiency of monofilament is 23% higher than for nylon and 7% higher than for monotwine, and the catch officiency for monotwine is 15% higher than for nylon. As would be expected, the transformation from numbers to weight favours the nets with the higher standard deviation.

The reliability of the catch efficiency ratios is difficult to assess. The errors caused by shortcomings in data and in assuming log-normal distribution selection curves for the fish caught with the head first are believed to be small. The assumptions about proportionality between mesh size and mean selection length and between mesh size and the width of the selection curves for all mesh sizes seem also likely to cause only relatively small errors, at least within the size range of cod normally caught by gill nets. The assumption that the selection index for the mean selection length is constant may be

more questionable. Experiments by RICKER (1949) indicate that small meshes may be generally less effective than larger meshes. How this applies to cod is, however, unknown. An obvious error is caused by not including fish caught in irregular ways in the fitting of the selection curves. Including them would have tended to reduce the calculated differences in catch efficiency which therefore may be overestimated.

One factor which probably has had some influence on the results, is that the cod were spawning, and they were accordingly thicker around the middle than non spawning cod. It is therefore possible that the selectivity of gill nets is somewhat different for non spawning than for spawning cod. Another factor which may be important is that the three types of nets were combined during the experiment in one setting. This may have produced relative catch efficiencies which are different from those one would have got if each setting consisted of only one type of net.

It is not known to what extent environmental factors, especially light conditions, have influenced on the relative catch efficiencies. Fishermen who have used monofilament gill nets, often claim that it is much more efficient compared with nylon nets than the results from Lofoten indicate. If this is true, different environmental conditions may provide at least some of the explanation, and more research is clearly needed to establish the importance of environmental factors.

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PUP PRODUCTION AND SUSTAINABLE YIELD OF WHITE SEA HARP SEALS

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ABSTRACT

BENJAMINSEN, T. 1979. Pup production and sustainable yield of White Sea harp seals. *FiskDir. Skr. Ser. HavUnders., 16*: 551–559.

Pup production from 1962 to 1965 was estimated by a survival index method from age composition of Norwegian samples of moulting harp seals collected in the southeastern Barents Sea from 1964 to 1972.

Pup production decreased from 130 thousand in 1962 to 98 thousand in 1965. From these estimates production was projected forward to give an estimate of 172 thousand pups produced in 1978, corresponding to a total stock of one year old and older harp seals of about 800 thousand. Both the projection and the number of adult females in the whelping patches estimated from Soviet aerial surveys give an annual increase of about 5% since 1968. The sustainable yield for 1978 is estimated at 98 thousand pups and 8 thousand one year and older animals.

INTRODUCTION

Populations of harp seals *(Pagophilus groenlandicus)* breed in the spring at Newfoundland-Labrador, in the Jan Mayen area of the Greenland Sea and in the White Sea. These populations are separate. The White Sea harp seal has an annual feeding migration into the Barents Sea and the Kara Sea and has been seen as far north as 79° in the eastern part of the Svalbard area in summer.

The harp seal has been exploited by aborigines for centuries along the coasts of the White Sea and the southeastern Barents Sea. Norwegian sealers started hunting harps in the White Sea in 1867, the catch increasing slowly to 40 thousand by 1900 (IVERSEN 1927). At the beginning of the 20th century large Russian ships were introduced in the hunt while the number of Norwegian ships increased. The resulting increased catch reached a maximum of 460 thousand in 1925 with a mean of 347 thousand per year in the period from 1923 to 1927 (YAKOVENKO 1967). After 1925 the catch decreased with a mean catch of 222 thousand seals taken per year in the period from 1933 to 1937. According to YAKOVENKO (1967) this drop could only be explained by a decrease in the size of the stock. Only small catches were

taken during the Second World War, and after the war Soviet catches increased to 195 thousand by 1950 while Norwegian catches in the southeastern Barents Sea were kept at a level between 10 and 35 thousand per year.

After 1950 the stock declined rapidly, and a quota of 100 thousand harp seals for the Soviet catch was introduced in 1955, being gradually reduced to 60 thousand in 1963. In 1965 a total quota of 34 thousand was put into force, of which Soviet landsmen were allocated 20 thousand and Norwegian ships 14 thousand seals. In 1977 the total quota was increased again to 50 thousand, 34 thousand to Soviet and 16 thousand to Norway. Adult females have been protected in the whelping patches since 1963, and the Soviet catch of one year old and older seals was stopped in 1965.

Data on age and sex composition of Norwegian catches of moulting harp seals in the southeastern Barents Sea have been collected since 1963. Most of the age samples (sexed and dated) have been collected by observers from the Institute of Marine Research, some age samples without information on sex and date have been taken by sealers.

The purpose of this paper is to estimate pup production from Norwegian age samples of moulting seals and project the female population forward in order to calculate the present sustainable yield of the White Sea harp seal population. The projection is compared to aerial photography estimates of the number of adult females in the whelping patches as presented to the Northeast Atlantic Seal Commission (Norwegian-Soviet Seal Commission) by Soviet scientists.

MATERIAL AND METHODS

Catches of harp seals in the White Sea and the Barents Sea from 1958 to 1977 are listed in Table 1. The data are based on reports to the Seal Commision. The Table shows that catches were substantially reduced, in particular the catches of one year old and older animals, after the introduction of reduced quotas and other regulations in 1965.

Age group frequencies of moulting harp seals from Norwegian samples in the Barents Sea from 1963 to 1976, which have all been reported to the Seal Commission, are shown in Table 2.

Production estimates were obtained by a «survival index method» (Sergeant 1971, Øritsland 1971, Benjaminsen and Øritsland 1975). The method involves a regression of the abundancy of successive year classes on pup catches of the same year classes. The survival index is expressed as the ratio of the relative frequency of each year class in individual samples to the mean relative frequency of the corresponding age group in all samples. To calculate the mean survival index for each year class, each age sample is weighted in proportion to the square root of the number of animals in the sample.

Table 1. Catches of harp seals in the White Sea and the Barents Sea from 1958 to 1977. Data on Soviet catches are from reports to the Norwegian Soviet Sealing Commission. (1 year + is catches of one year old and older animals).

	Norway		Soviet		Total	
	Pups	1 year +	Pups	1 year +	Pups	1 year +
1958	2 733	12 369	84 995	27 997	87 728	40 366
59	2 257	6 286	48 257	47 982	50 514	54 268
1960	2 474	8 222	60 579	28 736	63 053	36 958
61	2 903	8 254	41 827	51 676	44 730	59 930
62	1 325	6 981	67 633	39 327	68 958	46 308
63	405	12 944	54 861	7 603	55 266	20 547
64	3 109	11 477	47 008	15 771	50 117	27 248
1965	4 537	1 899	20 135	0	24 672	1 899
66	1 932	10 319	20 012	196	21 944	10 515
67	9 648	2 004	20 000	0	29 648	2 004
68	11 960	3 150	20 000	0	31 960	3 150
69	5 241	6 697	21 588	593	26 829	7 290
1970	4 230	8 734	24 328	1 262	28 558	9 996
71	7 028	1 596	26 666	1 002	33 694	2 598
72	4 229	8 209	30 635	500	34 864	8 709
73	5 657	6 661	29 950	813	35 607	7 474
74	2 323	5 054	29 006	500	31 329	5 554
1975	2 255	8 692	29 000	500	31 255	9 192
76	6 742	6 375	29 050	498	35 792	6 873
77	4 129	3 383	34 007	1 488	38 136	4 871

The survival indexes were calculated for age groups 1 to 5 in the Norwegian samples of moulting seals collected in the Barents Sea from 1964 to 1972. Frequencies of age group 1 were calculated from the number of seals in the total samples while frequencies of age groups 2–5 were calculated from the number of two year and older seals in the samples. By linear regressions of survival indexes on pup catches, average estimates of production were obtained from the intercepts of the regression lines on the X-axis. Production estimates for various mid-years were obtained by regressions of different year class intervals.

An estimate of the total number of productively mature females was obtained by dividing pup production by pregnancy rate. Starting with the most up-to-date estimate, the number of productively mature females for the next year was calculated by substracting catch and natural mortality and then adding recruitment. Pup production was then calculated by multiplying by the pregnancy rate. In this way production was calculated for successive years. Recruitment was calculated by starting with a production estimate, substracting catch and natural mortality each year to productive maturity.

Table 2. Age group frequencies of moulting harp seals in Norwegian samples collected in the Barents Sea from 1963 to 1976. *M* = male, F = female, U = not sexed.

Age group	1963	1964	1965		1968			1970		1972		1973	1974		1976	
	U	U	M	F	M	F	U	M	F	M	F	U	M	F	M	F
1	30	75	17	36	111	123	95	184	170	162	149	207	108	109	71	62
2	24	44	11	8	43	35	28	92	92	114	111	83	91	55	49	50
3	19	46	7	5	33	37	27	89	93	84	80	68	82	57	24	35
4	28	26	8	3	16	10	9	53	38	84	52	28	62	40	22	12
5	11	28	4	3	5	7	9	24	23	27	35	33	36	31	20	4
6	11	17	7	2	12	9	12	6	18	11	23	31	29	27	7	14
7	8	20	6	0	24	12	16	3	21	9	16	24	20	35	19	37
8	7	13	9	2	23	9	10	1	14	6	8	15	20	29	22	50
9	11	19	5	4	18	3	13	0	11	12	15	24	9	16	32	40
10	6	13	8	4	16	1	9	0	10	9	16	21	7	15	27	16
11	2	11	7	0	13	1	5	1	4	6	4	18	7	11	24	11
12	1	13	6	0	3	0	2	0	1	6	9	20	2	11	21	12
13	1	7	6	2	3	0	6	0	1	5	2	13	4	11	14	11
14	3	11	7	1	5	1	4	0	2	4	1	16	5	8	17	12
15	4	6	7	0	4	0	3	1	0	6	3	3	2	4	14	8
16	1	6	5	1	2	0	3	0	1	3	0	4	1	5	21	8
17	1	2	1	1	3	0	0	0	2	4	0	3	1	1	19	5
18	1	3	2	0	3	0	2	1	2	2	0	12	2	4	12	6
19	1	1	4	0	4	0	3	0	0	1	0	3	3	1	14	2
20	1	2	3	1	4	0	2	0	2	6	2	10	0	0	14	2
21	0	2	2	0	0	0	1	0	0	2	0	5	2	0	11	1
22	0	0	1	0	4	0	0	0	0	2	0	2	0	1	6	0
23	0	0	0	0	3	0	1	0	0	0	1	2	1	1	4	0
24	0	0	0	0	1	0	1	0	0	0	0	1	0	2	2	2
25	0	0	0	0	0	0	2	1	0	1	0	3	0	1	3	0
26+	0	0	0	0	3	0	0	2	0	4	0	3	2	2	8	0
Total	171	365	133	73	356	248	263	458	505	570	527	652	496	477	497	400

No attempt has been made to include any possible density dependent effect on age of sexual maturity, pregnancy rate or natural mortality.

Sustainable yield of pups can be estimated from the basic assumption that constant production requires an equilibrium between recruitment and mortality among productively mature females. For a stable population this may be expressed by the following equation:

$$\tfrac{1}{2} \cdot (B - C) \cdot S^a = \frac{B}{f} \cdot (1 - S)$$

where B is pup production, C is sustainable yield of pups, S is survival rate, a is median age of first whelping and f is fertility rate. A median age of first whelping of 5 years (YAKOVENKO and NAZARENKO 1967) was used in the calculations. No estimate of fertility rate or natural mortality is available for the White Sea harp seal. Therefore a fertility rate of 0.90 (ØRITSLAND 1971) and an annual natural mortality of 10% (MERCER 1978) as found for Newfoundland–Labrador harp seals, were applied. Age distribution of the catch of one year old and older seals is assumed synonymous with the population structure as is an equal sex ratio. A 1:1 sex ratio of pups is also assumed on the basis of unpublished Norwegian data.

RESULTS

Pup catches and survival indexes for the year classes from 1959 to 1971 are listed in Table 3. The table shows that high pup catches before 1965 give survival indexes well below 1.00, and that the reduced pup catches from 1965 to 1970 produce indexes higher than 1.00. Weighted mean indexes were calculated for the year classes from 1960 to 1969. These are plotted against the pup catches of their respective year classes in Fig. 1. The intercept of the regression line on the X-axis gives an estimate of pup production in the mid-year 1964 of 103 thousand.

Pup production estimates with their 95% confidence interval for different mid-years from 1962 to 1965 are listed in Table 4. The estimates show that pup production decreased from 130 thousand in 1962 to 98 thousand in 1965, with corresponding lower confidence limits of 94 and 74 thousand pups.

Estimated and projected pup productions from 1962 to 1978 are plotted in Fig. 2, showing that production increased from 98 thousand in 1965 to 172 thousand in 1978. Included in Fig. 2 are the number of adult females in the whelping patches estimated from Soviet aerial survey data. The two curves have the same shape, and both show a mean annual increase of about 5% from 1968 to 1976.

From a production estimate of 172 thousand, the sustainable yield in 1978 is calculated at 98 thousand pups and 8 thousand one year and older seals.

Table 3. Pup catches of the White Sea harp seal and the survival of corresponding year classes expressed by a survival index (frequency in sample/average frequency). Below the year of sampling is given the number of specimens and the weight given to the sample in calculating the weighted mean for 1–5 year old seals.

Year class	Pup catch $x10^{-3}$	Survival index					
		1964	1965	1968	1970	1972	Weighted mean
		368	206	867	963	1 097	
		1.3	1.0	2.0	2.2	2.3	
1959	51	1.43					
1960	63	0.82	0.68				0.76
61	45	0.86	0.65				0.77
62	69	0.72	0.42				0.59
63	55	0.69	0.59	0.58			0.62
64	50		0.86	0.59			0.68
1965	25			0.97	1.14		1.06
66	22			0.93	1.36		1.16
67	30			1.27	1.62	1.17	1.35
68	32				1.42	1.57	1.50
69	27				1.23	1.13	1.18
1970	29					1.35	
71	34					0.95	

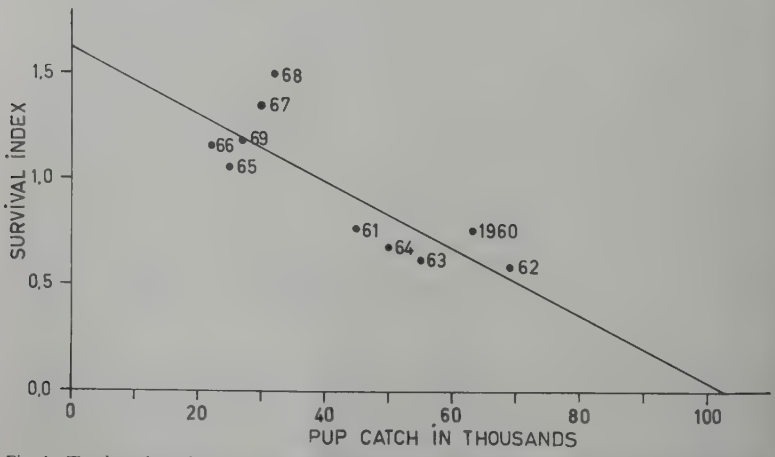

Fig. 1. Total catches of harp seal pups in the White Sea and the Barents Sea and the survival of the year classes 1960–1969 as indicated by weighted mean survival indexes from Norwegian samples of moulting seals collected in 1964–1972.

Table 4. Pup production estimates in thousands of harp seals in the White Sea calculated from linear regression of survival index on pup catch (*A*). *B* = the 95% confidence interval of pup production. r = correlation coefficient.

Period	Mid-year	Production		r
		A	B	
1960 – 65	1962	130	94 – 440	–0.87
1960 – 66	1963	118	94 – 186	–0.92
1960 – 67	1963	109	84 – 201	–0.86
1960 – 68	1964	103	79 – 211	–0.81
1960 – 69	1964	103	80 – 180	–0.82
1961 – 69	1965	97	74 – 194	–0.82
1962 – 69	1965	99	74 – 221	–0.82

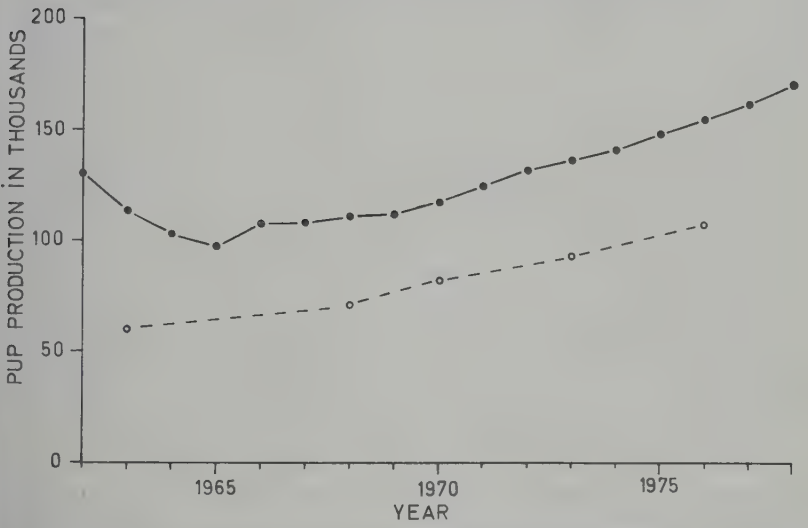

Fig. 2. Production of harp seal pups in the White Sea (closed circles) calculated up to 1965 by regression of survival indexes on pup catches. Production in 1966—1978 are calculated from a projection of the females population. For comparison, the number of adult females on the ice estimated from the Soviet aerial surveys is shown (open circles and stippled line).

DISCUSSION

The age and sex composition in the moulting lairs changes through the season as adult females gradually join the males and immature females through April and early May. Therefore the element of older animals in the Norwegian catches varies much from year to year, and survival indexes were only calculated for age groups 1 to 5.

BENJAMINSEN and ØRITSLAND (1975) showed that the moulting one year old harp seals of the Newfoundland–Labrador population to a large extent were segregated from older immatures and therefore were not sampled in any consistent relation to their abundancy in the population. The one year olds therefore were not included in their calculations of survival indexes. The one year olds in the Barents Sea, however, seem to be well mixed in with the older seals in the moulting lairs. The correlation between the frequencies of one year old seals in the Norwegian samples of moulting seals in the Barents Sea from 1964 to 1972 and the pup catches of these year classes is strong ($r = -0.93$).

The survival index method is only useful if pup production does not change too much during the period which is studied. The regression estimates also should be made only for periods with as high as possible variation in pup catches. In order to combine these two requirements it was decided to use only the age samples collected from 1964 to 1972 in the calculations. Survival indexes therefore could only be calculated for the year classes 1959 to 1971.

The pup production estimates obtained from survival indexes and the projection is about 50% higher than the number of adult females on the ice in the breeding layers estimated from aerial surveys. This difference may be explained by the fact that some females are always in the water. POPOV (1967) writes that on clear and windless days 45–55% of the adult females are on the ice in the day-time and 70–80% in the evening.

The projection is very sensitive to the input parameters. Mean annual natural mortalities of 9% and 11% instead of 10% would change the production estimate in 1978 from 172 thousand to 208 and 142 thousand respectively. A median age of first whelping of 6 instead of 5 years produce an estimate of 141 thousand pups in 1978.

A projection based on the lower limit of the 95% confidence interval indicates that production will increase from 74 thousand in 1965 to 91 thousand in 1978.

With the present total quota of 50 thousand, the White Sea harp seal stock will probably continue to increase at a rate of about 5% per year. The population is still small compared to the size at the beginning of the 20th century, and during the first decade the increase will probably not have any noticeable effect on natural mortality, age of sexual maturity or pregnancy rate. The abundance of fish in the Barents Sea, however, may have an effect on these vital parameters.

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AN ISOPOD AS INTERMEDIATE HOST OF COD-WORM

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ABSTRACT

BJØRGE A. J. 1979. An isopod as intermidiate host of cod-worm. *FiskDir. Skr. Ser. HavUnders.*, *16*: 561–565.

Ten cod *(Gadus morhua)*, caught at 30–50 m depth in the Froan area (64°N) on the Norwegian coast in October 1977, held an average of 53 cod-worm *(Phocanema decipiens)* larvae in their muscles. Stomach contents included fish, amphipods and isopods. Of 87 isopods, 84 were identified as *Idothea neglecta* and from these one *P. decipiens* larva was recovered. The findings suggest that *I. neglecta* is a significant food resource for coastal cod, and that this isopod also is a first intermidiate host of cod-worm.

INTRODUCTION

Cod-worm larvae (*Phocanema decipiens* Krabbe, synonyms: *Porocaecum, Terranova)* are found in fillets of cod *(Gadus morhua* L) and other commercially exploited benthic fishes from shallow waters around the North Atlantic. The larvae are causing severe economical problems for the fishing industry in several countries, particularly in areas where the grey seal, *Halichoerus grypus* (Fab.), is abundant. Together with other marine mammals, the grey seal is the final host of this parasitic nematode (YOUNG 1972).

Knowledge on the first intermediate host and its biology would give a better understanding of the distribution and incidence of cod-worm. Therefore the life cycle of *P. decipiens* has been extensively studied. SCOTT (1955) and MYERS (1960) have shown experimentally that *P. decipiens* eggs hatch in sea water. The eggs are hatched to larvae which are enveloped by a moulted cuticle (first stage cuticle) from which they cannot free themselves (SCOTT and BLACK 1960). These second stage larvae have a boring tooth (MYERS 1960).

Closely related parasitic nematodes have crustaceans as first intermediate hosts, and SCOTT (1950) suggested that also *P. decipiens* might develop in a crustacean. In 1958 SCOTT and BLACK (1960) collected 8500 Mysidacea in order to look for the first intermediate host of *P. decipiens*. Of the 71 nematodes found, all but 5 belonged to the genus *Contracaecum*. The remaining five were classified as belonging to the genera *Phocanema* or *Anisaksis*. Four of these were discovered in the mysids *Mysis mixta* and *M. stenolepsis*. The last

one came from a mysid which was so poorly preserved that it could not be identified. According to MYERS (1960) the nematode *Monohystera cameroni* Steiner, is a commensal of *Mysis mixta* and *M.stenolepsis*. Myers states that even under magnification this nematode resembles the larvae of *P.decipiens*.

SCOTT (1954) has demonstrated that fish can also become infected by eating other fish containing *P.decipiens*.

LOCALITY, MATERIALS AND METHODS

Froan is an offlying group of small islands, skerries and rocks northwest of the Trondheim fjord at about 64° latitude North, holding Norway's largest concentration of grey seals. It is estimated (personal observation) that at least 1000 grey seals inhabit the area from Halten light-house to Sauøy during the October-November breeding season. ØYNES (1964) roughly estimated that 300 female grey seals were breeding in the Halten-Froan area. FRENGEN and RØV (1976) assessed the number of pups born annually in the same area to be at least 300.

Within the Halten-Froan area at least 10 grey seal pups are born annually on Slettskjæra and Tindskjæra (64°06'N 09°08'E). On 12 October 1977 10 cod were caught by hook and line in shallow waters (30–50 m) near Tindskjæra. The otholits were preserved in a mixture of glycerol and formalin, the stomachs with contents were fixed and stored in 4% formalin, and the fish were salted.

In the laboratory the cod were filleted, and the parasites removed by examination under transmitted light. Stomach contents were sorted and crustaceans present were dissected under a binocular microscope. Some of the crustaceans were too decomposed to be identified and were not included in the analysis.

Isopods from the cod stomachs were identified according to SARS (1899), and nematodes from the isopods were identified by Bjørn Berland, Zoological Laboratory, University of Bergen.

RESULTS

The nematode infestation of the cod fillets was high (Table 1) with an average of 53 larvae per fish. They were all identified as *P.decipiens*.

From the stomach contents listed in Table 1, 114 amphipods and 87 isopods could be identified. Of the isopods, 84 specimens were identified as *Idothea neglecta* Sars, and 3 specimens as *I.baltica* (Pallas). In addition to the contents listed (Table 1), the cod stomachs contained large numbers of the nematode *Contracaecum aduncum* (Rudolphi).

Table 1. The infestation by *Phocanema decipiens* and stomach contents of cod caught at Tindskjæra, Froan, on 12 October 1977.

Cod No.	Age (years)	Number *P. decipiens*	Stomach contents				
			Idothea	Amphipoda	Fish	Other	Empty
1	5	84	+	+	+		
2	4	76	+		+		
3	3	9	+		+		
4	4	19			+		
5	5	73	+	+		+ [1]	
6	3	35					+
7	3	38		+	+		
8	4	14			+		
9	3	3	+	+			
10	5	177	+	+	+		

[1]) One *Munida rugosa* (Fabricius, 1775)

The 84 specimens of *I.neglecta* contained a total of three nematodes: two *C.aduncum* and one *P.decipiens*. No nematodes were found in the three *I.baltica*. A total of five nematodes were found in the amphipods, all being too small or shrunken for proper identification.

DISCUSSION

Benjaminsen, Bergfløt and Huse (1976) demonstrated that infestation of *P.decipiens* in cod was greater in shallow waters than at greater depths. Sars (1899) writes that *I.neglecta* is a benthic organism living at depths from upper sublittoral down to 20 fathoms (about 37 m). If *I.neglecta* is an important first intermediate host of *P.decipiens*, as suggested by this study, this may explain the apparent correlation between depth and the infestation of *P.decipiens* in cod.

Our knowledge of the life cycle of *P.decipiens* is still incomplete. However, the probable succession of events may be summarized in the following way: Eggs are excreted with the seal faeces and hatch in sea water to second stage larvae which are enveloped in their first stage cuticle. When eaten by an invertebrate first intermediate host (*e.g.* isopod) they are freed from their cuticle and probably moult to third stage larvae. Both second and third stage larvae have a cuticular boring tooth.

The larvae remain in the first intermediate host until it is eaten by a fish. The larvae, thus freed by digestion, penetrate the intestinal wall and migrate to muscle tissue where they encapsulate in their second intermediate host. If this fish is eaten by another fish, the larvae again migrate from intestine to muscle tissue and become encapsulated once more. In this case the fish acts as a carrying host, the larvae remaining unchanged in development although they may grow in size.

If, alternatively, the second intermediate or the carrying host is eaten by a mammal, the larvae rapidly moult to their fourth stage of development. These fourth stage larvae have well developed labia but lack the boring tooth. They are either attached to the stomach mucosa or lying free in the mucus. They later moult to their fifth stage of development and become sexually mature, thus completing the cycle.

The *C.aduncum* found in the isopods could either have been in the isopods before ingestion by the cod, or they could have penetrated the isopods within the digestive tract of the cod. Because of the quantities of *C.aduncum* in cod stomachs, this finding does not constitute evidence for amphipods as hosts of this nematode.

Working conditions during field work in 1977, particularly the time limits, prevented the use of a more appropriate collecting procedure for nematodes from the amphipods, *e.g.* to dissect out the nematodes while they are alive, and then to kill them in an extended position in hot alcohol or glacial acetic acid (Berland 1961).

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